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MEASUREMENTS OF PRIMARY PRODUCTION IN COASTAL SEA WATER USING A LARGE-VOLUME PLASTIC SPHERE

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ABSTRACT

A free-floating 20-ft diameter thin transparent sphere, with its center 5.5 m below the sea surface, was filled with nutrient rich water filtered free from plants and animals and inoculated with a natural population of coastal phytoplankters. The resulting phytoplankton "bloom" was then studied in this well-mixed water mass under near-natural conditions of temperature and illumination with the minimum of complications arising from grazing, sinking or lateral transport of the plant cells.

Daily measurements were made of temperature, light and photosynthesis and the water was analyzed for oxygen, carbon dioxide and all common micronutrients. The production of plant material was followed by cell counts and pigment values and by analyses for particulate carbon, nitrogen, phosphorus, carbohydrate, protein and fat.

The results have a bearing on nearly all aspects of marine primary productivity and are discussed in detail. In particular, the growth kinetics and chemical composition of a natural mixed crop have been related to the environment with the minimum of ambiguity. Growth was finally limited by nitrogen deficiency, although the plant biomass nearly doubled after nitrate became depleted, with a shift of metabolism to carbohydrate and fat synthesis. The composition of the plankton at various stages in a bloom is summarized by ratios involving carbon and chlorophyll *a*.

Differences between the results for photosynthesis obtained by the oxygen and C^{14} method have emphasized the importance of knowing photosynthetic quotient values and possible unlabeled sources of plant carbon. During an initial period of low illumination there was strong evidence for heterotrophic growth.

The principal species found in the "bloom" were *Skeletonema costatum, Thalassiosira nordenskiöldii, T. rotula, Gyrodinium fulvum, Glenodinium danicum, Nitzschia delicatessima* and *Asterionella japonica*. The last two grew very slowly and the two dinoflagellates only appeared after the nitrate was depleted.

INTRODUCTION

It is unnecessary to stress the difficulty of studying photosynthetic productivity in sea water that arises because of the impossibility of observing any one discrete body of water for a sufficient length of time. Valuable information can be obtained by observing the behavior of pure cultures of marine phytoplankton but such work is no adequate substitute for the study of the growth and decay processes that occur with mixed populations under natural conditions.

An obvious solution to the problem would be to impound sea water in a tank and valuable exploratory experiments of this nature were undertaken by Edmondson and Edmondson (1947) and Edmondson (1956). However, the use of a tank has several disadvantages unless it is very deep. The light-

ing of the water mass as a whole can be unrealistically high, and undesirable temperature increases usually occur. Furthermore, no precise "balance" of dissolved oxygen or carbon dioxide can be readily computed when there is a large surface area of water in contact with the atmosphere.

The thin plastic tube experiment proposed by Margalef (1956) would avoid some of this trouble, but in order to reduce wall-effects (the undesired growth of epigenous organisms, especially bacteria) one must have as large a volume to surface area ratio as possible. It is now common experience that a wall-effect from bacteria can be noticed within a very few hours in a small bottle and we may therefore assume that a container must be many feet in diameter before wall-effects can be neglected for a period of many days. A large container has the additional advantage that errors from accidental contamination are reduced.

To overcome most of the difficulties outlined above we have constructed a free-floating thin plastic sphere, 20 ft in diameter, suspended with its center a constant distance (5.5 m) beneath the sea surface. This plastic bag was connected to the surface by a comparatively narrow neck through which samples could be taken. The state of the water contained in the sphere approximated closely that of the surrounding sea water, both in temperature and in the conditions of illumination. An account of the construction of this equipment has already been published by Strickland and Terhune (1961). It was used in Departure Bay (49°20′ N, 123°50′ W), near Nanaimo, on the east coast of Vancouver Island, British Columbia.

The purpose of the present paper is to describe a phytoplankton bloom which was observed in the plastic sphere under these near-natural conditions. The production of such a bloom has enabled growth conditions to be studied without any of the ambiguities normally introduced by water movement. Further, the detailed analysis of the resulting crop has given the first extensive set of results applicable to detritus-free marine phytoplankton grown under natural conditions, that has so far been reported. Phenomena such as the succession of species and the effect on phytoplankton of nutrient environment were studied with the minimum of complications.

In one experiment the plastic sphere was torn after only 5 days but in the other (June–July 1960) 22 days of growth and decay were recorded before the equipment commenced to leak and this experiment forms the basis of most of the results reported in the present communication. We propose to repeat the experiment at least once more, and expect to be able to prolong it for many more weeks so that the decay processes of an initial bloom can be studied in greater detail. There is really no end to the number of such experiments that could be undertaken as each time different species of plant cells would doubtless develop. The present work, however, measures the production of a diatom crop which is quite typical of the spring bloom in temperate coastal seas.

In this experiment some difficulty was encountered with the stirring mechanism and it was not possible to keep all dead and dying plant cells in uniform suspension within the bag. In these circumstances one cannot equate the formation of soluble metabolites to the decrease of particulate matter sampled at the center of the bag. However, this limitation applied only to the last few days of the decay processes which followed peak phytoplankton production.

The authors would like to record their thanks to L. D. B. Terhune and others at the Pacific Biological Station, Nanaimo, for their work in designing, assembling and launching the equipment. We also wish to acknowledge the assistance given by the undergraduate student assistants, Wing Wai and John Yu, in the analytical program.

PROCEDURE AND METHODS

General procedure

The plastic bag was filled with water taken near the sea floor, about 350 ft from the low-tide shore line. The depth of the water at the intake varied with the tide between some 15 and 20 m. The water was pumped to land, filtered through a cloth-plate filter coated with diatomaceous earth,

and returned to the location of the bag (250 ft out in 11–16 m of water) by an all-plastic pipe system. Volumes were recorded with a water meter and a total of 125 m^3 of sea water was required to fill the bag.

After preliminary analyses the contents of the bag were "inoculated" with 4 m^3 of the surrounding sea water drawn from a depth of about 4 m. This water was pumped through an all-plastic assembly, and was strained through 320-μ mesh nylon netting to remove all but the smaller zooplankters.

The initial water in the bag was entirely free from animals and contained few if any plant cells. The chlorophyll *a* content of about 0.15 mg/m^3 was probably detrital, although there could have been a few microflagellates present. The inoculum was high in pigment (an average chlorophyll *a* content of 11 mg/m^3) and undoubtedly introduced some animal population into the bag. However, no significant zooplankton population developed during the course of the experiment and no chitin was detected analytically at any time.

The initial "background" level of particulate organic matter was undesirably high. The material consisted mainly of protein and we cannot explain its presence. Most probably there was a leak of diatomaceous earth at one stage in the filling, or detrital material of near-colloidal dimensions may have escaped filtration. The amount was very much less than in unfiltered sea water.

The inorganic nutrient content of the bottom water used to fill the plastic sphere was large and representative of the winter levels of concentration found in this area, which is one of the most fertile coastal regions of the world. Therefore, no artificial fertilization with silicate, nitrate, or phosphate was attempted.

As a daily routine, the depth of the plastic sphere was adjusted to a constant level by the suitable addition or removal of air from the buoyancy bell. The temperature and salinity of the water at the center of the bag and at the same depth in the sea alongside the bag was measured first thing each morning. A plastic Nansen reversing bottle with protected thermometer was employed to measure temperature and to take samples for salinity determination.

At about 0900 hr each day samples were taken in a plastic Van Dorn bottle and used for water analyses. The water was filtered at once through a Millipore HA membrane filter and suitable aliquots of the filtrate stored at –20°C in the dark until ready for analysis. Separate samples were drawn for oxygen, pH and alkalinity determinations, which were performed immediately.

Measurements of the attenuation of light in the sea and in the bag were carried out in the mid-morning and mid-afternoon. At about 1030 hr an 8-L sample was taken in Van Dorn bottles and well mixed in a polyethylene aspirator. Nitrogen was passed through the water, if necessary, to reduce the concentration of dissolved oxygen to below the saturation level and then the water was passed into 300-ml B.O.D. bottles for the measurement of photosynthesis. Some bottles were placed in a stainless steel holder suspended at a point 2 ft above the center of the bag on the stirring line and were left in the bag for 24 hr (1200 to 1200). Other bottles were illuminated in a laboratory incubator under constant (artificial) light conditions for a period of less than 6 hr.

At 1330 the water in the bag was sampled for the analysis of particulate matter. Samples were taken at the mid-point of the plastic sphere, using a Van Dorn bottle, and were mixed and stored in a 20-L polyethylene bottle. Filtration of this sample was commenced without delay.

Occasionally samples were taken from several depths and analyzed for pigment and dissolved oxygen, *etc.* in order to check on the uniformity of distribution of metabolites within the sphere.

Determination of dissolved substances

Full details of all analytical methods are given by Strickland and Parsons (1961). The following brief summary indicates the general techniques that were used.

Salinity was measured by an electrical conductivity salinometer, oxygen by the Winkler method, pH using the Beckman

model GS meter and a glass electrode standardized by standard phosphate buffer at pH 6.87, alkalinity by the Anderson-Robinson method (Anderson and Robinson 1946), silicate by the method of Mullin and Riley (1955a), nitrite by the method of Bendschneider and Robinson (1952), nitrate by a modification of the procedure described by Mullin and Riley (1955b), and phosphate-phosphorus by a modification of the method of Robinson and Thompson (1948). Total soluble phosphorus was determined as phosphate after wet oxidation wtih perchloric acid (*cf.* Hansen and Robinson 1953). Soluble organic phosphorus was measured as the difference between the total phosphate in a sample passed through a Millipore HA filter and the inorganic phosphate in the same sample. Particulate and soluble reactive iron and ammonia were estimated as outlined by Strickland and Austin (1959). The method used for manganese was based on the catalyzed oxidation of the leucobase of malachite green by periodate, as developed by one of the present authors (see also Yuen 1958). Copper was determined as the colored diethyldithiocarbamate complex which was extracted directly into carbon tetrachloride. Soluble organic nitrogen was estimated by evaporating 25 ml of filtered water and subjecting the residue to Kjeldahl oxidation. The ammonia in the residue was then determined absorptiometrically, as above, and the result corrected for any ammonia found in the initial sample.

The change of total carbonate-carbon in the bag was obtained from precise measurements of the change in pH, knowing the total alkalinity of the system, and using a modification of the Buch tables given by Strickland and Parsons (1961) with graphical interpolations. As only changes in carbonate concentration were being measured in an isolated system, a very precise alkalinity determination was not necessary (*cf.* Strickland 1960).

Determination of particulate matter

Details of all methods (with the exception of the enumeration of phytoplankton cells) are described by Strickland and Parsons (1961). A brief summary of the procedures will be given here for the convenience of the reader.

All sea water samples were first filtered through a nylon net with a mesh size of 300 μ to remove any large particles of extraneous detritus introduced during sampling. The concentration of the particulate matter was accomplished by filtering the water through a Millipore type AA membrane filter, previously treated with magnesium carbonate (Parsons and Strickland 1959). When sufficient sea water had been filtered the Millipore filter was removed and the concentrated particulate material was washed from the surface with a small quantity of 3.0% saline. The suspended particulate matter and magnesium carbonate were then further concentrated by centrifugation and the supernatent liquid was discarded. The resulting residue was used for the determination of carbon, carbohydrate, crude fibre carbohydrate, protein, fat, nitrogen, and phosphorus.

Plant pigments

Chlorophyll *a*, *b*, *c* and carotenoids were measured as described by Richards with Thompson (1952) using the Millipore filter technique to concentrate the phytoplankton cells described by Creitz and Richards (1955). Extinctions were measured in 10-cm cuvettes. A correction for turbidity was made using the extinction at a wave length of 7,500 A, multiplied by a predetermined factor to allow for increasing light scatter at decreasing wave lengths.

Carbon

Particulate carbon was determined by wet oxidation with potassium dichromate in concentrated sulphuric acid by a modification of the procedure described by Johnson (1949). The decrease in the extinction of dichromate solutions at a wave length of 4,400 A served as a measure of the amount of oxidizable carbon.

Protein and nitrogen

Particulate protein was determined by two methods. The first involved Kjeldahl digestion of the sample and an estimation of the ammonia using Nessler's reagent, Johnson (1941). Nitrogen values determined by this

method were converted to protein values by multiplying by a factor of 6.25. The second method involved the hydrolysis of the particulate protein with 6 N HCl at 100°C for 6 hr, followed by a colorimetric determination of the hydrolyzed protein using 2,5-hexanedione and Ehrlich's reagent, as described by Keeler (1959). The method was standardized using pure dry casein. Nitrogen values were obtained by dividing by a factor of 6.35. Unlike the tyrosine methods for protein, the Keeler technique involves the reaction of 8 amino acids and ammonia in a hydrolysate. However, results still depend on the amino acid spectrum of the algal proteins which differs from species to species and which cannot be expected to resemble that of casein exactly.

Carbohydrate

Particulate carbohydrate was determined by the anthrone reaction using the reagents employed by Hewitt (1958) and measuring the light absorption of the colored solution developed at a wave length of 6,200 A. Additional absorptions were measured at wave lengths of 5,500 A and 6,500 A in order to determine, qualitatively, the presence of hexuronic acids and pentoses. The method was standardized with glucose. "Crude Fibre Carbohydrate" was also determined by the anthrone reagent on a concentrated residue after consecutive treatments with 1.25% sulphuric acid and 1.25% sodium hydroxide in a boiling water bath.

Fat

The amount of fat present in the particulate matter was determined by a modification of the method described by Mukerjee (1956). The method specifically measures fatty acids. Results obtained by the use of this method may be less than values obtained by an ether extraction technique. The method was standardized with stearic acid.

Particulate phosphorus

Particulate phosphorus was determined as phosphate after a wet oxidation with perchloric acid (*cf.* Hansen and Robinson 1953). The particulate phosphorus is defined as that retained on a Millipore HA filter.

Enumeration of phytoplankton cells

Phytoplankton cells were counted using a Unitron inverted biological microscope. Samples of sea water were preserved in 2% neutral formalin and counts were made on 5- or 10-ml aliquots of sea water without prior concentration of the cells. Samples were counted at magnifications of 50×, 100×, and 400×. Duplicate counts of 20 fields made at equal intervals across the diameter of the cylinders (2.6 cm in diameter) normally agreed within 10%. An approximate estimate of the average cell volume of each of the principal species present was made by direct microscopical measurement of the dimensions and shapes of the cells. All cells were counted, living or dead, provided that they were sufficiently intact for ready identification.

Phytoplankton cell numbers, as such, were of limited interest because of the enormous size differences between one species and another. For better comparison total cell numbers were converted to total cell volume (μ^3) by the following experimentally determined factors: *Nitzschia delicatessima*, 500; *Skeletonema costatum*, 1,900; *Glenodinium danicum*, 3,600; *Thalassiosira nordenskiöldii*, 11,000; *Thalassiosira rotula*, 35,000, and *Gyrodinium fulvum*(?), 150,000. (In the other experiment, of only 5 days duration, the following additional factors were used: *Coscinodiscus radiatus*, 12,500; *Coscinodiscus centralis*, 7,350,000.) To convert the resulting algal volumes to organic carbon a factor of 0.1 was employed (*cf.* Strickland 1960). The evaluation of total carbon from cell counts by the above procedure is, at best, very approximate. However, results of cell counts alone can be most misleading unless some such attempt is made to translate cell numbers into a measure of biomass.

Measurement of radiant energy

Incident radiation was measured with an Eppley pyrheliometer situated on a hill about 400 yd from the plastic sphere. Photosynthetically active radiation (3,800–7,200 A) was assumed to be 50% of that measured by the pyrheliometer, and is reported in cal/cm^2/min (ly/min, *cf.* Strickland 1958).

Mean daily light intensities are the averages of the values recorded between sunrise and sunset.

Optical extinction coefficients of the water in the bag and the surrounding sea were determined from measurements with an underwater light meter and deck cell. Both cells were fitted with 2 mm of Schott BG. 12 blue glass, giving a maximum response of photocell-filter combination near to a wave length of 4,300 A. The attenuation of photosynthetically active light was estimated from these extinction coefficients using the data collected by Jerlov (1951).

Mean daily light intensities at the center of the plastic bag were calculated using the extinction coefficient of the surrounding water through the first 3 m, and then the extinction coefficient of the water in the sphere through a further 3 m. When the morning and afternoon extinction coefficients differed markedly their mean value was used. It must be emphasized that the radiation intensities obtained by this method are only very approximate but relative values from day to day are strictly comparable.

Measurement of photosynthesis

Measurements of photosynthesis were carried out by both the light and dark bottle oxygen method and a modification of Nielsen's C^{14} technique (see Strickland and Parsons 1961). All rates were measured using duplicate "light" bottles and a single "dark" bottle. The initial oxygen concentration was determined so that the net oxygen changes and respiration values in dark bottles could be evaluated.

The constant light intensity incubator used in this work held the B.O.D. bottles lying horizontally in black painted trays and cooled by running tap water. Samples were illuminated from above by blue and green fluorescent lamps emitting 0.1 ly/min of radiation as measured by a pyrheliometer.

No account was taken of possible periodicity effects in photosynthesis as these are thought to be quite small at latitude 49°N (Doty 1959).

One would suppose from the work of Fogg (1958) and others that $C^{14}O_2$ uptake experiments of more than about 6-hr duration would give errors due to the secretion of labelled material. It was impracticable, however, to conduct a series of short exposures in the sphere throughout each day and extrapolation from a single 6-hr period to a full 24 hr of light and dark was too inaccurate to be of use. Therefore we resorted to 24-hr radiocarbon experiments, on the assumption that at low light intensities the results would be tolerably accurate, as already reported by Rodhe (1958). We confirmed this experimentally by comparing the sum of the uptakes in two half-day exposures with that of a full 24-hr exposure in the bag. At the higher light intensity in the incubator there was very poor agreement between the rates found with 6- and 24-hr exposures, again supporting the findings of Rodhe (1958). At this higher light intensity plants were metabolizing many times more rapidly in the incubator than in the bag, and dividing once or twice in the 24-hr period of continuous illumination. Under such conditions the secretion of metabolites and "light fatigue" of the plant cells would be expected to be pronounced.

Experiments to measure the relative rate of photosynthesis as a function of illumination were carried out with the C^{14} method and the wire-screen attenuators described by McAllister and Strickland (1961). Natural daylight was used as a source of illumination during the period between about 1000 and 1400 on cloudless days. The light intensity over this period was nearly constant.

RESULTS

The salinity of the water in the bag was 27.00‰ and its temperature initially 11°C. The transmission of light through the polyvinyl chloride plastic and its supporting coarse-mesh nylon netting was greater than 75%, excluding any effects from direct shading by the supporting buoyancy bell and cradle. Temperature changes in the water inside the sphere closely followed those of the surrounding sea water. This is illustrated by Figure 1 which shows the total daily amount of solar radiation at the sea surface, the temperature at 5 m depth in the sea, and

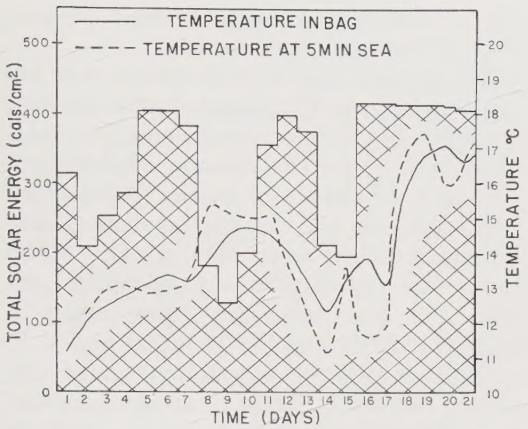

FIG 1. Total solar radiation and the water temperature inside and outside the plastic sphere.

the temperature at 5.5 m in the bag. It is interesting to note the delay of some 4 days before the sea temperature showed the influence of large changes of incoming radiation. The temperature of the water in the bag followed that of the sea outside with a lag of only about one day.

Most of the data obtained during the present experiment are summarized graphically, and generally the limits of variation are indicated by vertical lines or by the size of the plotted points. The confidence limits embrace the 95% probability region or are thought to approximate this value. Certain important ratios of metabolites and of metabolites to photosynthetic rates, *etc.* are collected in the tables and will be discussed later. The precision of these ratios varies greatly but their significance may generally be judged by the number of significant figures quoted. Some other results appear to have little obvious significance and will be summarized briefly in this section.

No chlorophyll *b* was detected in any analyses and the level of animal carotenoid (astacin) pigments was very low and erratic. The apparent presence of the latter may have been an analytical artifact. Copper was present in a concentration of 0.048 μg–at Cu/L which did not change throughout the three weeks of the experiment. The concentration of reactive manganese varied between 0.01 and 0.04 μg–at Mn/L with little obvious pattern, although there was a maximum just before the main phytoplankton growth period started (day 8). Soluble reactive iron changed little in concentration being in the range 0.07 to 0.12 μg–at Fe/L. The amount of particulate reactive iron was quite large. Initially present at 0.7 μg–at Fe/L it decreased in quantity to one-third of this value by day 12. The concentration thereafter increased to the initial level. The significance of this behavior, if any, is not clear. The decrease roughly paralleled that of soluble nitrogen but more experimental work is necessary before definite conclusions are possible.

The initial concentration of soluble organic phosphorus in the sphere was appreciable (0.3 μg–at/L) and seems to have increased slowly during the growth of the phytoplankton crop and then more rapidly as the crop decayed, reaching a value as high as 0.55 μg–at/L. Three anomalous results were obtained in this series of determinations and more work is required before any definite pattern can be stated. The concentration of soluble organic nitrogen showed a similar increase throughout the experiment (about 2 up to 7 μg–at N/L) but there was no marked correlation with the algal growth behavior. The precision of this method is relatively low (±0.8 μg–at N/L or worse) which may have masked any subtle relationships.

In a well-stirred conserved system the decrease of total dissolved nitrogen or phosphorus must be equal to the increase found in the particulate matter. The analytical results of losses and gains in the present work gave tolerable agreement until after day 17. Then serious discrepancies resulted which showed that stirring was insufficient to keep dead and dying cells in suspension. The decrease of particulate matter after day 17, therefore, represents both the true dissolution of solids and their removal from the bag center by settling. Although analytical results on the particulate material, *per se*, are still valid, no conclusions can be drawn from *changes* of concentration (as sampled at the center of sphere) for the last 5 days of the experiment.

The useful life of the plastic bag was ter-

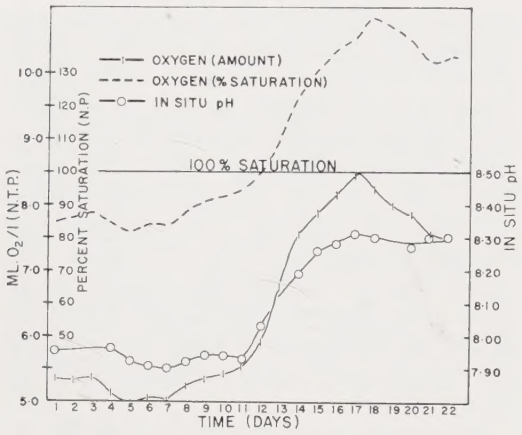

FIG. 2. Changes in pH and dissolved oxygen.

minated by tears near the neck (at day 5 in one trial and day 23 in the main experiment). As the salinity of the surrounding sea water was generally 2 or 3‰ less than the water in the bag the entry of outside water was easily detected by precise (conductivity) salinity measurements.

DISCUSSION

The net production of organic matter during the course of the main experiment is illustrated by Figure 2, which records the change of pH and oxygen concentration in the plastic sphere. The percentage saturation of oxygen (at atmospheric pressure) shows the striking degree of supersaturation often reported in the literature and attributed to the effect of photosynthesis. A value of nearly 150% was recorded in the present work. The subsequent decrease of oxygen concentration (after day 17) was mainly due to physical desaturation processes as no corresponding decrease of pH occurred.

The main phytoplankton species present at various stages in the experiment are shown in Figure 3. The use of algal weight (derived from algal volume assuming a mean density of unity) enables one to comprehend the relative contribution of each species to the overall primary production. The total cell count exceeded that of the named species by up to 25% but the unnamed species represented a much smaller addition to the biomass than numbers alone would indicate. *Asterionella japonica* was the most conspicuous of the minor constituents.

The growth rate of each species was not uniform but over the period of most constant growth mean division times could be evaluated. Values for the diatoms *Skeletonema costatum*, *Thalassiosira rotula*, *Thalassiosira nordenskiöldii*, and the dinoflagellate *Glenodinium danicum* were very similar (30–38 hr). The dinoflagellate *Gyrodinium fulvum* (?) was noticeably more rapid in growth (22 hr) and for an initial period *T. rotula* increased with a doubling time of only 19 hr. The cell numbers of all species eventually showed a decrease which we attribute to the rapid sinking of dead or dying cells (ref., *e.g.*, Gross and Zeuthen 1948; Steele and Yentsch 1960). *T. rotula* passed its peak of metabolic efficiency somewhere between days 8 and 11. This could reflect either a marked sensitivity to the concentration of nitrate or be the result of an increase of water temperature from 12 to 15°C. One cannot rule out the possibility of an inhibition by the increasing concentration of *Skeletonema* cells. *Nitzschia delicatessima* was the only organism to grow to any degree under markedly unfavorable conditions (a doubling time of over 80 hr) and this species commenced to die off soon after the depletion of nitrate at the end of day 13 (Fig. 4). *Asterionella japonica* persisted in small numbers throughout most of the experiment but was obviously living under conditions so unfavorable as to bring cell division almost to a standstill.

The growth rate of *S. costatum* decreased as soon as nitrate disappeared from solution but, statistically, the cells were capable of one further division. *T. nordenskiöldii* grew more vigorously and divided twice before the cells commenced to die. By contrast the two dinoflagellates only began to increase rapidly after the nitrate was exhausted and *Gyrodinium fulvum* survived in fair condition until the end of the experiment. The above observations give a striking illustration of the kind of conditions that bring about a "succession of species" in nature (*cf.* Conover 1956; Margalef 1956). We are unable to explain the kinks in the curves for *T.*

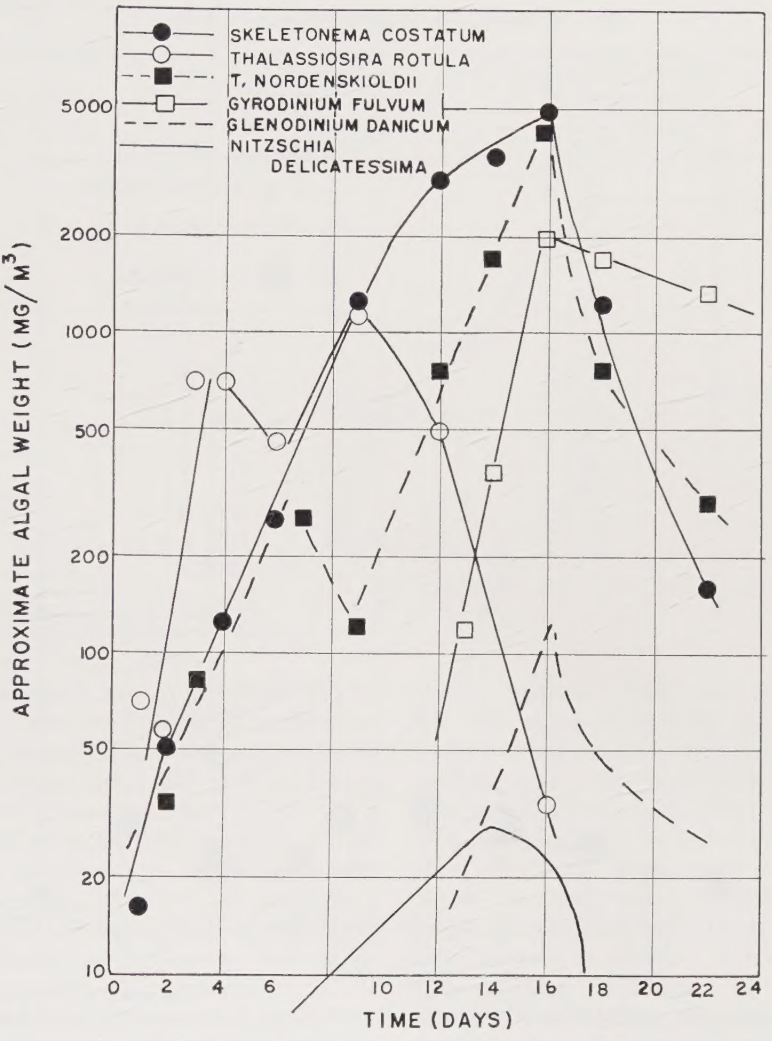

FIG. 3. Changes in the algal weight of the main phytoplankton species.

rotula and *T. nordenskiöldii* (there was a similar very high point for *Skeletonema* at day 3, not plotted). There must have been an error either in sampling or in counting brought about by a change in mean chain length, and hence a contagion factor, for the species concerned.

Iron, copper, and manganese were clearly not limiting nutrients for plant growth and reactive silicate was initially present at such a concentration that it never became depleted, despite the crop being predominantly diatoms. One would infer from our results that the initial Si:N ratio in sea water would have to be less than 2:1 (on an atom basis) for silicon to become a limiting nutrient in a diatom bloom. It is interesting to note the small but significant rise in silicate concentration after day 16 which indicates that a fraction of the silicon in a diatom is very labile (*cf.* Jørgensen 1955a). Subsequently there was only very slow remineralization. In considering this fact and the remineralization of nitrogen (see later) it must be remembered that the present experiment is unrepresentative of nature in that no regeneration processes could occur as a result of grazing (*cf.* Cushing 1959).

The initial ratio of nitrogen to phosphorus in solution was 9 (on an atom basis) or 10 if

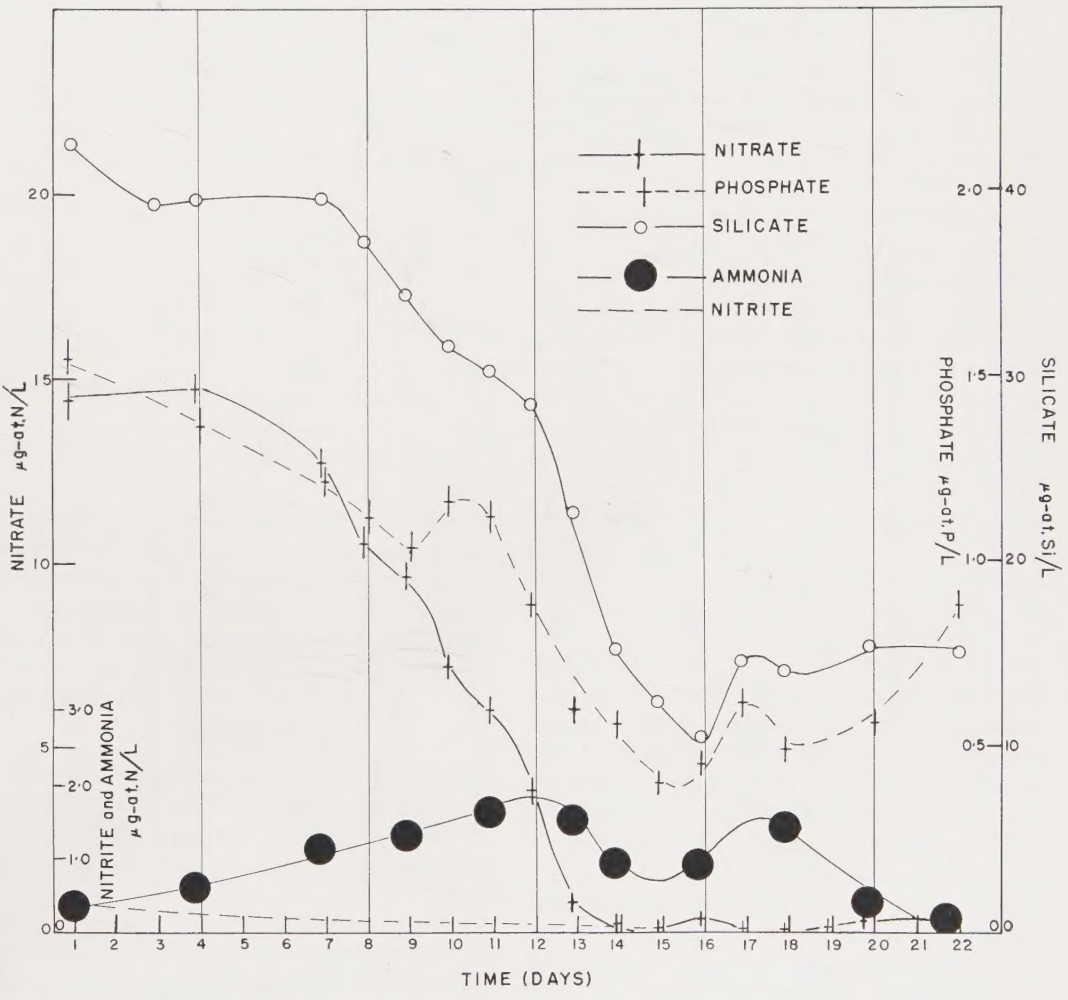

FIG. 4. Changes in the concentration of nitrate, nitrite, ammonia, reactive phosphate and reactive silicate.

we consider only nitrate and inorganic phosphate. On the assumption that growing plants withdraw these elements from sea water in the mean atomic ratio of 15:1 (Cooper 1937, 1938) one would expect to find nitrate removed before phosphate, as was indeed the case (Fig. 4). Furthermore, the tendency for phosphate to continue to decrease in concentration after all the nitrate has gone, as found in cultures of open Pacific Ocean water by McAllister, Parsons, and Strickland (1960), was also shown in this experiment with coastal water. It will be seen from Figure 4 and from the analytical data given in Table 2, that the ratio of nitrogen to phosphorus in the growing cells was variable, being quite low during the first part of the experiment and then increasing to approach the "classical" 15:1 value.

Phosphorus was not a "limiting nutrient." The comparatively labile nature of its incorporation in phytoplankton (Gest and Kamen 1948; Goldberg, Walker and Whisenand 1951; Rice 1953; Rigler 1956) and the rapidity with which it can leave dead cells (Hoffmann 1956; Golterman 1960) is reflected by irregularities in the curve in Figure 4. In particular there was a small but definite *increase* in the amount of the element in solution between days 9 and 10. Cells appear to have stored an abnormally large amount of phosphorus (see Table 2), some of which

TABLE 1. *Ratios involving photosynthetic rates*

Day	Ratio: Rate. (O_2 gross) / Rate. (C^{14}) (PQ=1)		Ratio: Rate. mg C/hr (O_2 gross) / mg chlorophyll *a* (PQ=1.3)	Productivity index[2] from gross O_2 (PQ=1.3)
	Bag	Incubator	Incubator	Incubator
1	–	–	1.3[1]	–
2	–	–	1.2[1]	–
5	–	3.3	1.65	–
6	2.4	–	–	–
7	1.8	–	–	–
8	2.1	3.3	1.6	–
9	2.7	–	–	–
10	1.9	2.9	1.75	0.9
11	1.9	3.3	1.6	0.75
12	1.9	3.3 *Mean 3.3*	1.45	0.75
14	1.7	–	1.6	0.75
15	2.2	2.0	1.65	0.75
16	1.5	1.7	1.05	0.55
17	2.0	1.4	1.05	0.4
18	1.5	1.9 *Mean 1.75*	0.95	0.2
19	1.7 *Mean 1.95*	–	–	–

[1] Values using carbon-14 rate measurements.
[2] Carbon measured by direct chemical method.

was then liberated during a period of low illumination and increasing temperature. Phosphorus was obviously lost more rapidly than nitrogen from dead cells and this is also shown by the ratios given in Table 2.

Nitrite nitrogen, initially present at 0.35 μg-at N/L decreased to one-fifth of this value in the first 14 days. It is not possible to say whether or not nitrite was incorporated into phytoplankton (*cf.* Harvey 1953; Bongers 1956) or oxidized by bacteria.

Whereas nitrate nitrogen was consumed rapidly and in a more or less regular fashion it is interesting to see that there was an increase in ammonia concentration (Fig. 4) until day 13 and a significant increase in the amount of soluble organic nitrogen. Ammonia was clearly not used in preference to nitrate when the latter was in great excess (*cf.* Harvey 1940) although when nitrate became depleted there was some indication that ammonia could be scavenged from solution and might, in this instance, have been providing *Gyrodinium fulvum* with its most readily accessible supply of nitrogen. There was little or no indication of any nitrogen remineralization, but this is not surprising considering the time scale suggested by the work of Von Brand, Rakestraw and Renn (1939), Spencer (1956) and others and the fact that some plant cells were still living and removing available forms of the element until the end of the experiment.

As noted by several workers (*e.g.*, Harvey 1953; Rodhe 1957) the growth rate of phytoplankton can be quite rapid even when all nitrate has been removed from a medium and cells exist for one or more divisions on their reserves of protein. The present work gives striking illustration of this fact as nearly half of the final organic matter in the phytoplankton bloom was produced after nitrate depletion. Any attempt to predict the kinetics of natural population growth using the concept of a "limiting concentration" of nitrogen (or phosphorus) therefore has little meaning unless the past history of the phytoplankton crop is also known. There may, of course, be conditions where the supply of nutrients is just balancing consumption but for how long such an unstable equilibrium could exist in nature, especially in coastal regions, remains to be shown.

There is a shortage in the literature of direct comparisons between the oxygen and C^{14} methods of measuring photosynthesis and many of the results quoted are for pure cultures. In the present work ratios were

measured by the two methods whenever practical, both at the center of the plastic bag for 24 hr and in the constant light incubator for shorter periods. In Table 1 the ratios between *gross* oxygen liberation and radioactive carbon uptake are presented with no assumptions as to what is being measured.

The ratios are disconcertingly large, but they can be reduced if a large photosynthetic quotient (*PQ*) is allowed and if the $C^{14}O_2$ method is assumed to measure net photosynthesis in cells which have a high respiration rate. The highest *PQ* and respiration values normally used are about 1.35 and 15% respectively which would give a ratio of 1.6 at moderate light intensities. (This subject is fully reviewed by Strickland 1960.)

The ratios measured by the bottles at the center of the bag averaged 1.95. They fell into two distinct groups in the incubator, where there was from 3 to 10 times more illumination. Values before day 14 (and nitrate depletion) averaged 3.3 and the four values after day 14 had a mean of 1.75. It is generally supposed that nitrogen deficient cells have a high respiration rate and hence low rate of net photosynthesis (Ketchum, *et al.* 1958) but these last four results do not indicate that the C^{14} results are usually low, unless *PQ* values are also very small. The ratio of 3.3 in a nitrate rich medium is even less easy to explain. One is compelled to assume very high values for the *PQ* of diatom cells taken from a nitrate rich medium at low illumination and exposed for a few hours to comparatively high light intensities. The whole question of a correct *PQ* value is of much greater importance in marine studies than is generally admitted, especially if one wishes to make an accurate estimate of carbon uptake from oxygen measurements.

It is interesting to note that the depletion of nitrate had no significant effect on the 24-hr ratios determined in the plastic bag. These values may be slightly high due to the prolonged period of $C^{14}O_2$ uptake.

With all these results we suspect that ratios are greater than they should be, even having regards to likely experimental errors and high *PQ* and respiration values. It is possible that in coastal water the C^{14} method is giving low results due to the photosynthetic assimilation of non-labeled forms of carbon (Smith, Tatsumoto and Hood 1960; and see also Strickland 1960 for a discussion).

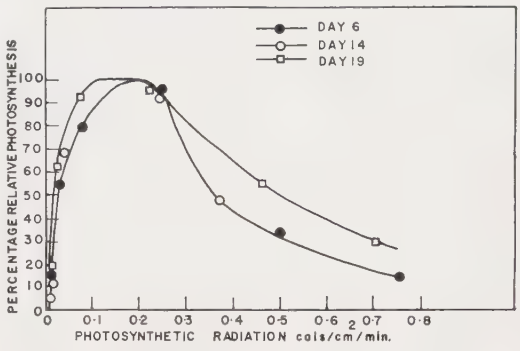

FIG. 5. Relative rate of C^{14} assimilation as a function of radiation intensity.

The relative photosynthetic rates (*f*) *vs.* illumination values (*I*) for the populations in the sphere on days 6 and 14 have been plotted on the same curve in Figure 5. This is very similar to that given by Ryther (1956). At day 19, when *Gyrodinium fulvum* comprised about half the population, the values lay on a slightly different curve. There was then the greater tolerance to high light intensities to be expected from a dinoflagellate (*e.g.*, Ryther 1956) but the curve at lower intensities still resembled that for the diatom population. It will be seen that the light intensity of 0.1 ly/min used in the incubator was at approximately the optimum value. Mean light intensities at the center of the bag did not exceed 0.055 ly/min and photosynthesis was therefore always roughly proportional to light intensity.

Back extrapolation of *f vs. I* curves to zero light intensity should indicate the amount of plant respiration, if the assumptions made by Nielsen and Hansen (1959) are justified. The values so obtained, about 10%, are reasonable.

Figure 6 shows the increase in carbon in the plastic bag from day 1 to day 22, as measured by both oxygen and C^{14} methods, again with no assumption of *PQ* values or the significance of the C^{14} measurements. The increase on day 13, and hence the total for all subsequent days, may be low as there

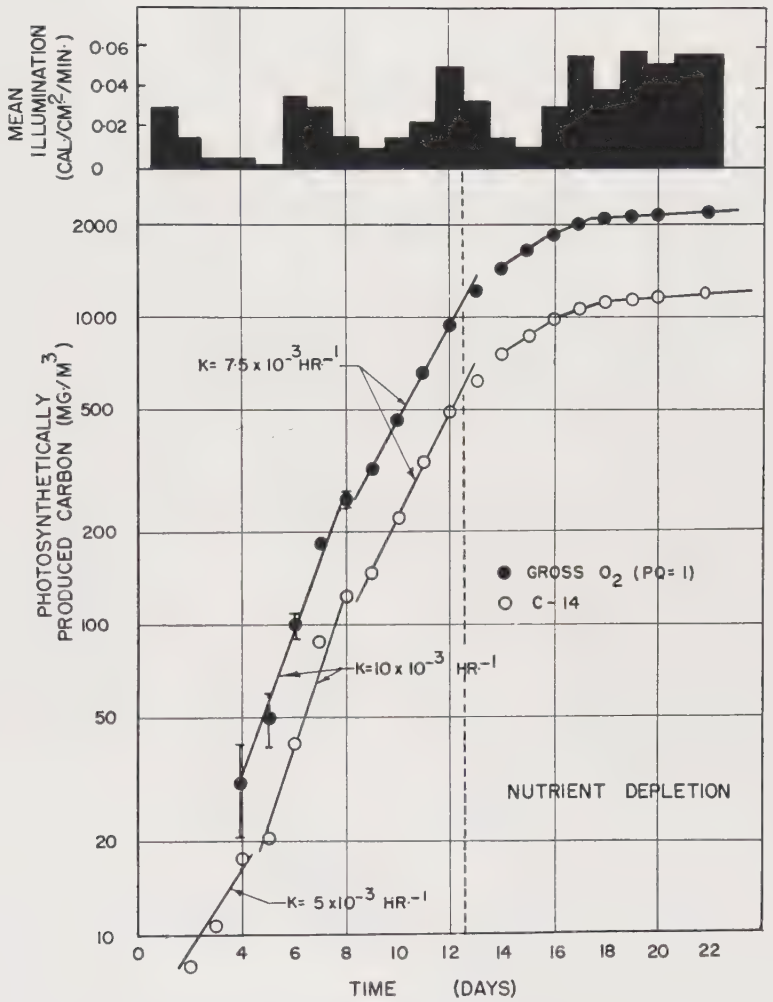

FIG. 6. Photosynthetic carbon fixation in the plastic sphere as a function of time under natural lighting.

was poor stirring that day with a temporary loss of plant cells. The curves are parallel and their slope can be used to evaluate logarithmic growth constants. The values given in Figure 6 (base 10) probably reflect changes in temperature and light intensity (see the histogram for mean daily illumination at the bag center). After the end of day 15, severe nitrogen shortage brought about a reduced growth rate and results no longer have much meaning, because cells were sinking below the sampling point in the bag.

The most fruitful way to examine the effect of nutritional changes on the photosynthetic metabolism of algal cells is to expose them to constant light intensity in an incubator and find either the rate of carbon increase per unit of chlorophyll *a*, or the productivity index, defined by Strickland (1960) as:

$$\frac{\text{hourly rate of carbon increase}}{(\text{amount of plant carbon}) \times (\text{illumination in ly/min})}$$

Both these values are given in Table 1, using the gross photosynthetic rate measured by oxygen evolution and an assumed *PQ* of 1.3. There was no significant change in the photosynthetic potential of the cells from day 1 to day 15, having regards to the general magnitude of experimental errors.

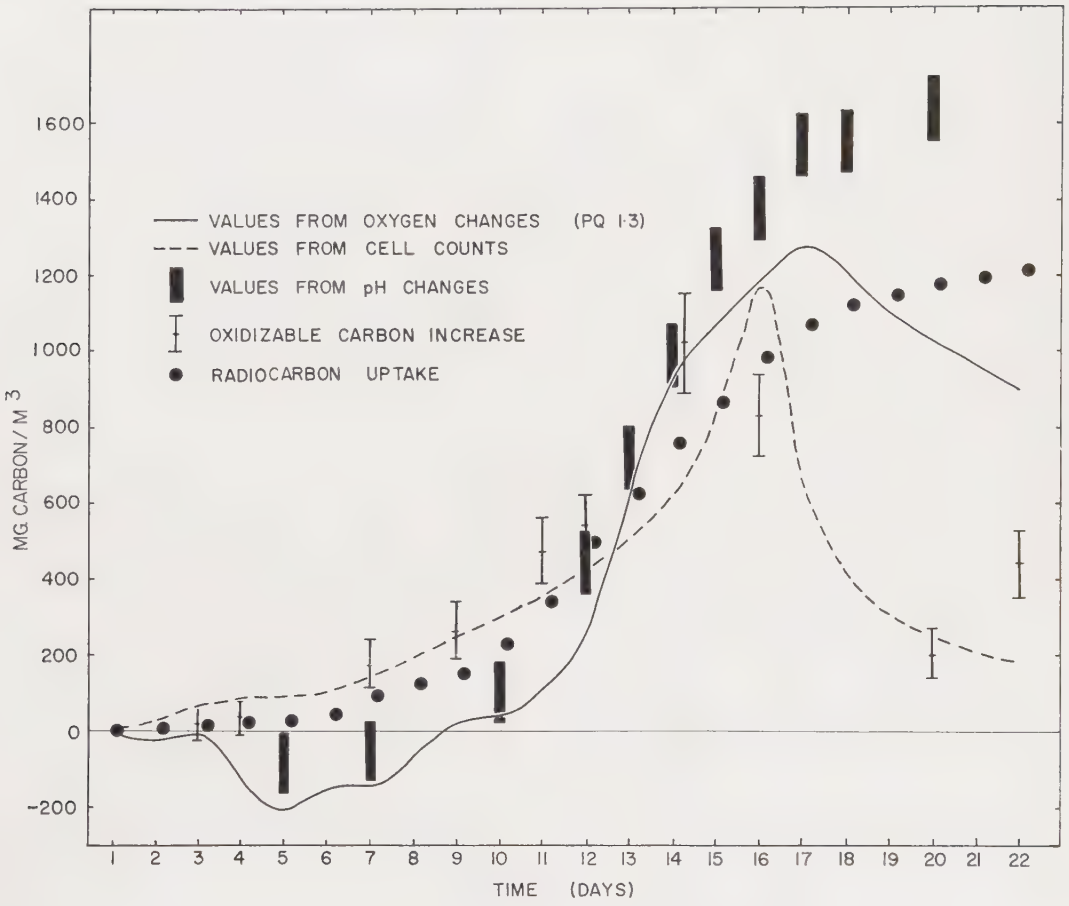

FIG. 7 Net production of carbon as measured by five independent methods.

The gross rates, per unit of chlorophyll *a* at optimum lighting, were very much lower than the rates reported by Ryther and Yentsch (1957), although they were within the range found in the literature (Strickland 1960) and comparable to the values found by McAllister, *et al.* (1960) in the open Pacific Ocean.

These productivity index values are the first of their kind to be reported, and are near to many of the values inferred from the literature (Strickland 1960). The high value at day 10 may be significant but was not reflected in the corresponding figure for the rate per unit of chlorophyll *a*. Similarly the decrease of productivity index at the end of the experiment was much more pronounced than the corresponding decrease in the chlorophyll ratios, but this would be expected because a large amount of detrital carbon was accumulating. In particular it should be noted that the loss of nitrate at the end of day 13 had no effect on either ratio. Only at day 16, when the mean nitrogen content per cell was probably less than a half of its peak value, did the photosynthetic processes, as reflected by these ratios, become seriously impaired. At the same time cells commenced to settle out rapidly (Fig. 3).

There was no evidence in our experiment for the situation reported by Ryther, *et al.* (1958) where the growth of a diatom bloom in nitrogen deficient water was static as the result of a sizable amount of photosynthesis during the day being compensated for by respiration during the hours of darkness.

The net production of organic particulate carbon in the plastic bag was estimated by

five methods and the results are shown together for comparison in Figure 7. The full line shows the values calculated from changes of dissolved oxygen in the bag, assuming a *PQ* of 1.3. Results are probably low after day 15 or 16 due to physical losses of oxygen from the supersaturated system. The dotted line is a measure of plant carbon derived from cell counts and, as mentioned earlier, is only very approximate. The bars show the range of individual results estimated from changes of total carbon dioxide content. This is the most direct method of all but unfortunately not as precise as could be wished. The solid circles mark uncorrected data calculated from the uptake of radiocarbon. These results were used in preference to the gross oxygen photosynthesis data because they formed a more complete set, and did not involve assumptions as to respiration rates and photosynthetic quotients. However, it is by no means certain that C^{14} data represent true net photosynthesis; they may well be too low. Finally, there are the experimentally measured oxidizable carbon results corrected for initial detritus. These results are entered as horizontal dashes with the 95% confidence limits indicated by vertical lines. Any excretion of soluble organic compounds during plant growth would make these results lower than they should be and this would also influence the ratios in Table 2.

Ignoring the measurements derived from dissolved oxygen and pH, the agreement between the other three estimates was as good as could be expected for much of the time. The two direct methods, carbon analysis and algal volume, finally showed decreases due to the settling of cells, although there was appreciable net synthesis going on inside the bag until at least day 20.

The various measurements of carbon during the first few days of this experiment gave the most anomalous results and they merit closer investigation. The dissolved oxygen content of the bag first *decreased*, representing the consumption of over 200 mg C/m^3, but there was no corresponding decrease of particulate carbon. A wall effect would not be expected so soon in equipment of this size (in the other experiment the oxygen decreased steadily from the first day) so presumably, much of the oxidation was by nonproliferating bacteria in suspension, using a substrate of dissolved organic carbon. This was borne out by the high but fairly constant respiration values found in the dark bottles used in photosynthesis experiments.

Not only was there no decrease of particulate matter, corresponding to the net consumption of oxygen in the bag, but the increase in photoplankton carbon, as estimated by cell volumes and changes of chlorophyll (see later) was appreciable and very rapid during the first 4 to 5 days. This increase, mainly in *T. rotula* and *Skeletonema*, could not be accounted for by photosynthesis, as the radio carbon uptake data predicted very much smaller values for carbon (one quarter or less). The most likely explanation, therefore, is that during the period of very low illumination at the start of this experiment (see Fig. 6) heterotrophic growth from dissolved organic carbon was a large fraction of the total growth. The effect was not detected in the 5 days of the second experiment, when the illumination was quite high. But at the beginning of the main experiment, a very heavy bloom of flagellates in the surrounding water prevented light entering the bag for several days. It is interesting to note that what little photosynthesis did occur during this period took place in a normal manner. The photosynthetic rate, per unit of chlorophyll *a*, in the incubator had about the same value as found during the rest of the experiment (Table 1).

Heterotrophic growth of algae is well established (Saunders 1957) and has been studied in marine diatoms by Lewin and Lewin (1960). Conversion of dissolved substrate to algal carbon can be high if the behavior of *Chlorella* is representative (Myers and Johnston 1949; Samejima and Myers 1958). Several workers have stressed the probable importance of heterotrophy in phytoplankters (Rodhe 1955; Wood 1956; Bernard 1958) but we believe the present work to be the most direct demonstration of its occurrence in marine phytoplankton under

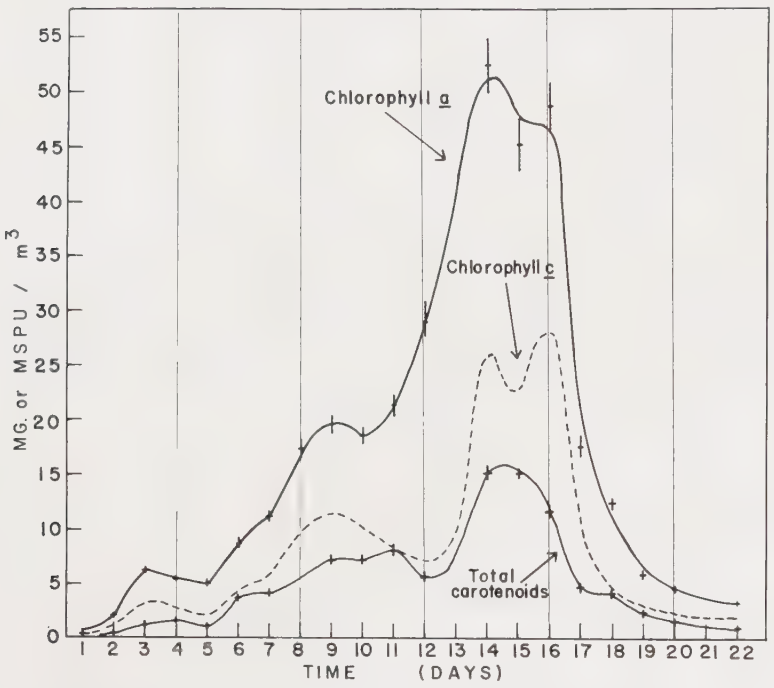

FIG. 8. Changes in the concentration of plant pigments.

conditions resembling those found at the base of the euphotic zone.

Variations of chlorophyll *a*, chlorophyll *c*, and total carotenoid concentration at the center of the bag are shown in Figure 8. The chlorophyll *c* curve roughly parallels that for chlorophyll *a* for most of the experiment, giving values about 50–60% of the chlorophyll *a*, in terms of MSP units and milligrams respectively. Between days 11 and 13, however, the ratio of chlorophyll *c* to chlorophyll *a* was much smaller, decreasing to 25%. This period coincided with the predominance of *Skeletonema costatum* in the bloom and we have found (unpublished work using pure cultures) that this species has what is probably an abnormally high chlorophyll *a* content and a low chlorophyll *c* to chlorophyll *a* ratio for a diatom. The large chlorophyll *a* content of *Skeletonema* would explain the very high maximum value found in the present experiment (50 mg/m^3). In the open ocean, a natural culture in water of essentially the same initial nitrate concentration bloomed to only 26 mg/m^3 chlorophyll *a* at its peak (McAllister, Parsons and Strickland 1960).

The first few days of the experiment are particularly interesting. In 3 days the chlorophyll *a* concentration increased from 0.4 to 6 mg/m^3. If we estimate carbon from cell volumes, the ratio of carbon to chlorophyll *a* is found to change from 25 to 11 in the first 3 days, which is reasonable for a surface population recovering its pigment content in a nutrient-rich, relatively dark environment. The remainder of the chlorophyll increase must be associated with a rapid development of cells during this initial period. Ratios calculated using photosynthetically produced carbon data were impossibly low which, as mentioned earlier, supports the suggestion of some heterotrophic growth.

The sudden decrease of chlorophyll after day 16 was striking and much more than would be expected from a decrease of cell numbers alone. The possible presence of "detrital chlorophyll" in nature is a matter of some importance in field studies. Odum, McConnel and Abbott (1959) could find no

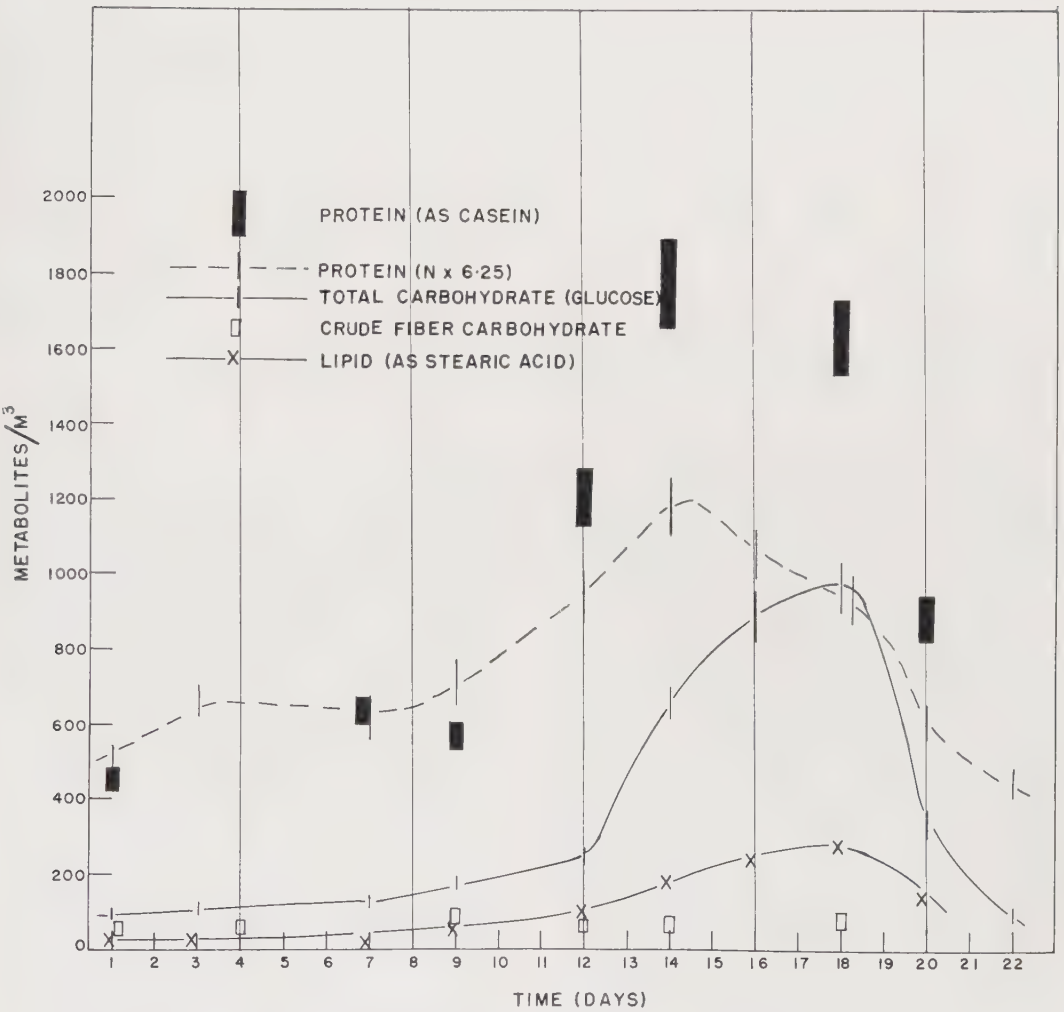

FIG. 9. Changes in the concentration of major metabolites.

spectrophotometric indication of such material. The present experiment seemed to be an excellent opportunity to investigate the matter. We measured the complete pigment spectrum, in 90% acetone, of the populations on day 12 when cells were growing with full vigor and day 18 when many cells were dead or dying but found no evidence for phaeophytin or phaeophorbide pigments. There was a noticeable broadening of the long-wave-length chlorophyll *a* peak in the extract made on day 18, and a slight shift to shorter wave lengths (6,650 A to 6,630 A). We have seen this effect in old laboratory cultures and it is reminiscent of the *in vivo* behavior reported by French and Elliott (1958). There is little likelihood, however, that such small changes would have any practical significance in marine pigment analysis. However, chlorophyllides, which could conceivably occur in decomposing plant tissue, have similar absorption spectra to chlorophylls and it also remains to be proven whether the detrital chlorophyll from faecal pellets is in the form of phaeopigments and hence may give misleading results in nature.

The composition of the particulate matter in the sphere, in terms of major metabolites, is summarized in Figure 9. In order to esti-

TABLE 2. *Ratios involving carbon*

Day	Si[1]/C	Protein/C	Protein[2]/C	Carbohydrate/C	Lipid/C	C/P	C/N	C/N[2]	N[2] (atoms)/P
7	–	0.66	0.89	0.2	–	19	9.5	7	6
9	1.0	0.72	0.76	0.3	–	17	9	8.5	5
12	0.6	0.78	1.4	0.3	0.15	23	8	4.5	11[3]
15	0.65	0.65	1.3	0.7	0.2	28	10	5	12.5[3]
18	–	0.65	1.8	1.35	0.4	40	10	4	25
20	–	0.43	1.9	0.7	0.55	35	15	3.5	23
Value suggested by Strickland (1960)	0.8	–	–	–	–	40±15	–	6±2	14.5

[1] Calculated from the decrease of reactive silicate.
[2] Values from the absorptiometric protein method, standardized with casein.
[3] The ratio had a maximum of about 15 on day 13.

mate the amounts of carbon, protein, carbohydrate, phosphorus, *etc.* in living phytoplankton it was necessary to subtract from the amounts found on a given day, the amounts of each metabolite present initially in the water used to fill the sphere and, further, to assume that this initial "background" concentration of detrital material did not change throughout the experiment. Almost certainly such an assumption is not fully justified, although there is reason to suppose that settling of detritus was comparatively slow. Errors from this source were most significant in the earlier part of the experiment and ratios such as those given in Tables 2 and 3 had little precision until at least day 7 or 9.

There was a considerable discrepancy between the amount of protein obtained by the two chemical methods. Some of this difference undoubtedly arises because the amino acid spectrum of algal protein is not the same as that of casein, but we would not expect from our work on pure phytoplankton cultures (unpublished) that the differences would have been so great. Evidence from the "balance" between dissolved and particulate nitrogen in the bag pointed to the Kjeldahl nitrogen values being too low. A similar poor balance between nitrate lost from solution and nitrogen found in growing algae has been reported by Yentsch and Vaccaro (1958) but we are at a loss to explain the matter and more work is desirable. In the meantime, we have reported both sets of data in Figure 9, Table 2 and Table 3 and suggest that the colorimetric protein values are probably nearer to the "correct" results until at least day 12.

Crude fibre carbohydrate in the bag never exceeded a few per cent of the total phytoplankton carbohydrate. This confirms our (unpublished) findings for pure phytoplankton cultures and for natural coastal populations at the time of heavy diatom blooms. A quite different analysis is found for water containing much detritus, when as much as 80% of the total carbohydrate may be present as crude fibre. (There was about 60% in the detrital carbohydrate initially in the water of the present experiment.) An analysis for crude fibre is one of the best rapid chemical indicators for detritus, as distinct from living plant cells, in the sea.

The most striking feature shown by Figure 9 is the way in which the lipid and the carbohydrate (mainly glucose) in the plant cells increased when nitrate became depleted from solution on day 13 (*cf.* Spoehr and Milner 1949; Bongers 1956; Fogg 1957). Between about days 13 and 17 fats and sugars were almost the sole products of photosynthesis.

The classical conception of diatoms containing large reserves of fat is not borne out by the present work. When cells were in a dying condition in nutrient depleted water their lipid content was higher than earlier in the experiment, but was still less than 20% of the dry weight (see Table 2, assuming about one-third of the dry weight of a diatom is carbon). In the sea, near the surface, nitrate depletion doubtless occurs frequently and

TABLE 3. *Ratios involving chlorophyll* a

Day	C / chl. *a*	C / Carotenoids[2]	N / chl. *a*	N[1] / chl. *a*	P / chl. *a*	Carotenoids[2] / chl. *a*	Protein / chl. *a*	Protein[1] / chl. *a*	Carbohydrate / chl. *a*	Lipid / chl. *a*
7	15	43	1.6	2.2	0.81	0.36	10	14	3	–
9	13	37	1.5	1.6	0.80	0.36	11	10	4	–
12	19	100	2.4	4.2	0.83	0.19	15	27	5.5	3
15	22	70	2.2	4.5	0.78	0.31	14	28	15	4
18	56	160	5.9	16	1.4	0.36	37	100	76	22
20	49	150	3.3	15	1.4	0.33	21	93	33	27
Values suggested by Strickland (1960)	30	40	–	7±3	0.75±0.2	–	–	–	–	–

[1] Values from the absorptiometric protein method, standardized with casein.
[2] Total carotenoids in MSPU.

hence diatoms collected by net tows may often be expected to have their maximum lipid content (*cf.* Barker 1935). However, it is difficult to believe from the present work that the presence of fat assists diatoms in maintaining their buoyancy to any great extent.

The ratios of elements and metabolites to carbon and chlorophyll *a* at various stages in the phytoplankton bloom are given in Tables 2 and 3 respectively. The ratios involving carbon (the direct oxidizable carbon data were used) illustrate the relative changes in composition of the phytoplankton with time. The values involving chlorophyll *a* are important mainly because this pigment is the only convenient measure of plant material in sea water, as distinct from animals and detritus. Data such as those in Table 3 show the limits within which the plant carbon, nitrogen, metabolites, *etc.* can be estimated, knowing the pigment content of a water sample. Clearly each possible mixed algal population in nature, at every stage of its growth, will give rise to different ratios so that the value of any particular one is limited. Nevertheless, as pointed out by Strickland (1960) there are still very few relevant data of this kind available for marine phytoplankton. The results given here are a useful beginning, especially as they apply to a mixed diatom population growing under near-natural conditions. For comparison, the approximate mean values for marine crops suggested by Strickland (1960) are given at the bottom of each table.

It is unfortunate that the precision of the ratios measured during the early part of the experiment is not as high as could be desired, but the data for days 7 and 9 are approximately correct for a diatom population growing under low illumination in nutrient rich waters. The data for day 12 apply to a vigorously growing and rapidly dividing bloom, about to strip the nutrients from the water. On day 15 the results apply to algae at the end of their growth period in nitrogen-deficient water. By day 18 there were many dead and dying cells, and on day 20 little living material was present at the bag center, except dinoflagellates.

The Si:C ratios given in Table 2 are some of the few to be reported for a live natural population and are of the order to be expected from results cited in the literature. The decrease from day 9 to day 12 may be real, supporting the observations made by Jørgensen (1955b).

Most of the other ratios in Tables 2 and 3 are self-explanatory and illustrate the trends that have already been discussed. The increase in the ratios involving chlorophyll *a* after day 15 reflects the rapid loss of this pigment from dead or dying plant material, a loss more nearly paralleled by that of phosphorus and total carotenoid, than by any other of the measured variables.

The co-variation of chlorophyll *a* and the carotenoids is indeed remarkable and supports the detailed observations made by Haskin (1941) on *Chlorella* and our own (unpublished) work on pure marine cultures.

Except for day 12, when there was a preponderance of *Skeletonema costatum*, which we have found to have a relatively low carotenoid content, the ratios were very constant and similar to the values found for mixed coastal populations in Departure Bay at all times of the year. There was no evidence of either the particulate nitrogen values or the ratios in Table 1 being functions of the carotenoid-to-chlorophyll ratio, as has been reported by Ketchum, *et al.* (1958) and Yentsch and Vaccaro (1958). Why there should be this discrepancy between their well-established laboratory results and the present large-scale experiment is not clear. Of course, conditions were not identical and this emphasizes the dangers of extrapolating from laboratory-scale results or even, to a lesser extent, from the present experiment to phenomena taking place in the sea under completely natural conditions.

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MEASUREMENT OF ORGANIC CARBON IN SEA WATER[1]

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ABSTRACT

An apparatus and procedure for precise measurement of organic carbon in sea water is described. The method, sensitive at < 1 mg/L, entails wet combustion of 200-ml samples of sea water and infrared CO_2 analysis.

INTRODUCTION

The importance of studying total organic matter in sea water has been documented by Keys, *et al.* (1935). Current studies of organic production in the sea (Steemann-Nielson 1952; Odum and Hoskin 1958; and Ryther 1959 among others) may be enhanced by a convenient and precise method for determining total organic carbon in sea water. The very small concentrations of organic carbon and the high concentrations of salt in offshore waters have hindered the development of a satisfactory method. Difficulties with present methods of total organic carbon analysis may be classified into two interrelated categories: 1) complexity of procedure and 2) errors caused by loss or contamination of organic matter. These weaknesses have been discussed in detail by Kay (1954) and Barnes (1959). A new method for precise determination of total organic carbon in salt water, eliminating some of the difficulties found in previous methods, is presented here.

METHOD

A water sample was placed in a combustion cell; the inorganic carbonates removed; the organic compounds oxidized to CO_2; and the CO_2 measured by infrared absorption. Determination of CO_2 in an infrared analyzer has great sensitivity and lacks interference from other gases found in sea water such as chlorine, oxygen, and nitrogen. A Beckman Listen Becker infrared CO_2 analyzer (model 15A), a combustion unit, a KOH tube for removing CO_2, and a gas circulating pump were connected together by ⅜-in. stainless steel tubing and metal bellows valves (Fig. 1). The usual compound for sealing threaded connections was not used because of possible organic contamination. Instead, finely powdered teflon suspended in water proved adequate for lubricating and sealing connections. The pump, which needed no lubrication, was a metal bellows (Fulton Sylphon Division, Knoxville, Tenn.) driven by an eccentric arm and powered by an electric motor. The system was leakproof and free of organic materials which could contaminate samples. The heavy glass combustion unit was connected to leakproof metal bellows valves with Cenco metal-to-glass connectors which provided access to the cell for entering the sample and reagents. The combustion cell was sealed by closing the valves before placing the cell in a heated water bath to oxidize the sample.

To avoid possible errors caused by concentrating the water samples, potassium peroxide, effective in relatively dilute solution, was used as the oxidizing agent. This oxidant has been used in 200-ml samples of fresh water by Osburn and Werkman (1932) and by Battley (1957). Potassium peroxide is an effective oxidant at high temperature but not at room temperature. John Noakes at the A and M College of Texas is currently conducting independent research to determine the effectiveness of potassium peroxide as an organic matter oxidant in sea water.

Procedure

These steps were followed for routine analysis (italicized letters refer to Figure 1):

1. A 200-ml sea water sample was placed in the combustion cell *e* with 0.5 ml of 33% phosphoric acid, 4 gm of $K_2S_2O_8$, and a teflon encased magnetic stirring bar. The cell was connected to valves at *d* and the entire unit attached to the analyzer.

[1] Research under contract with the Office of Naval Research, NONR 375 (11), and supervised by Howard T. Odum for study of Metabolism of the Laguna Madre of Texas. These data are a portion of work for a graduate degree.

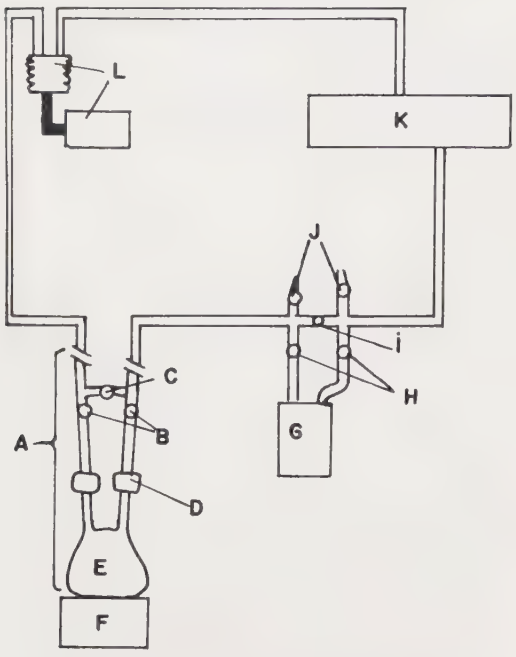

FIG. 1. Schematic diagram of apparatus for organic carbon analysis. Small circles represent Hoke helium-tested, leakproof, bellows valves. *a* is the detachable combustion unit; *b* seals the unit during oxidation when the unit is detached. After oxidation is completed, the unit is again attached to the system. Then, *c* is opened and the CO_2 removed from the system before *b* is opened; *d*, Cenco metal-to-glass connectors, permit the separation of the glass combustion cell *e* from the metal portion of the combustion unit. *f* is a magnetic stirrer; *g* a container with KOH for CO_2 adsorption; and *h*, *i*, and *j* are valves which route the flow of gas through the KOH at *g* to the atmosphere through *j* or only through *i*.

2. CO_2 was removed by pumping CO_2-free air over the sample while the sample was being vigorously stirred. Refer to Figure 1 for the proper adjustment of the various valves necessary to accomplish this.

3. The combustion unit was sealed and placed in a 100°C water bath for 60 min; then cooled to room temperature.

4. The combustion unit was reattached to the system unopened and all CO_2 removed from the system. The unit was then opened (the valves at *h* must be closed and *i* opened), and CO_2 in the combustion unit allowed to reach equilibrium in the entire system. Pumping and stirring were continued for 5 min.

TABLE 1. *Carbon recovered from reagent blanks and sea water blanks*

	Carbon/sample (mg)
Reagent blanks	0.31
	0.32
	0.33
	0.32
Sea water blanks	0.48
	0.47
	0.47
Sea water minus reagent blanks	0.16
	0.15
	0.15

5. Pumping and stirring were discontinued. Pressure was equalized by opening a valve at *j* before the CO_2 concentration was recorded. During oxidation of the sample, pressure was built up by release of oxygen and other gases (Osburn and Werkman 1932). This pressure artificially increased the reading on the infrared analyzer and therefore was released to obtain an accurate reading. However, when the pressure was released the volume of escaped gas had to be measured as this gas included some CO_2. The volume of gas was usually quite small and was trapped by running a rubber hose from a valve at *j* into a water-filled, 100-ml graduated cylinder which had been inverted in a beaker of water. The CO_2 lost with the escaped gas was computed by assuming that the CO_2 in the gas was identical to that remaining in the system.

6. The CO_2 was adsorbed in KOH for 30 sec with the stirring mechanism turned off. This step eliminated the CO_2 from the gas phase of the system but did not appreciably remove CO_2 from the sample. Valves were turned to by-pass the KOH chamber. Then the gas in the closed system was circulated and the liquid sample stirred for several minutes to pull the dissolved CO_2 from the sample into the gas phase.

7. Steps 5 and 6 were repeated until all CO_2 had been removed from the sample and measured.

Standardization

The instrument was standardized by attaching a plastic tube between the valves at

TABLE 2. *Carbon recovered from known dry weights of* Chlorella *added to sea water*

	Chlorella added (mg)	Carbon/sample (mg)	% carbon
Infrared Method	10.5±0.2	4.43	42.2
	10.6±0.2	4.42	41.7
	8.0±0.2	3.47	43.0
	10.3±0.2	4.35	42.2
	14.2±0.2	5.94	41.8
Corcoron's Method			41.6
			43.5
			37.7

TABLE 3. *Carbon recovered from field samples during April, 1960. All data have had reagent blanks subtracted*

Source of sample	Carbon (mg/L)			Salinity (‰)
Aransas Pass (flood tide)	1.4	1.3	1.5	33.0
Baffin Bay	80.0	91.5	—	51.3
Baffin Bay (filtered)	26.3	38.7	—	51.3
Laguna Madre	14.3	13.2	17.3	43.0
Redfish Bay	6.3	6.5	6.1	29.5

j and injecting various known amounts of pure CO_2 into the system with a tuberculin syringe, and constructing a curve for each of several gain sensitivities of the instrument. Care was taken to keep the sensitivity of the instrument below the level at which errors could arise due to water vapor interference.

RESULTS

To obtain sea water low in organic matter, aerated sea water from the Gulf of Mexico was filtered and placed in a darkened cabinet for several weeks. Known amounts of organic matter were added to test the effectiveness of the method. Reagent blanks were determined by using $K_2S_2O_8$ and phosphoric acid in double distilled water (Table 1). *Chlorella*, obtained from Dr. J. Myers, was used as a naturally occurring type of organic matter with an approximately known amount of carbon. Results of the infrared carbon analysis of *Chlorella* are compared in Table 2 with results obtained by Dr. W. McFarland who determined the organic carbon content of identical *Chlorella* using a modification of the wet combustion method described by Corcoron (1957).

The 200-ml field samples were placed in 500-ml Erlenmeyer flasks and immediately frozen in a dry ice and alcohol bath. The samples were kept frozen in an ice chest prior to being placed in the combustion cell. Between uses, Erlenmeyer flasks were cleaned with a hot solution of sulfuric acid and dichromate and stored with the tops covered by aluminum foil. Values obtained from some Texas coastal bays are reported in Table 3.

It is uncertain whether or not the infrared method provides 100% detection and measurement of all types of organic matter. The agreement between the results of the infrared method and the wet combustion method with samples of *Chlorella* indicates the method is probably satisfactory for productivity measurements where changes of organic content are due to living plankton organisms. An indication of the sensitivity and precision achieved with the infrared method may be obtained from the data in Tables 1 and 2. The method is capable of measuring organic carbon concentrations of less than 1 mg/L as shown in the values for "sea water minus reagent blanks." The replicates of *Chlorella* samples have a range of less than 2%.

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ECOLOGICAL AND PHYSIOLOGICAL STUDIES ON MARINE NEMATODES FROM A SMALL SALT MARSH NEAR WOODS HOLE, MASSACHUSETTS[1]

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ABSTRACT

Some physiological experiments have been performed on some marine nematodes from a soft-bottom community where they are numerically the most abundant group of the meiofauna. They appear to account for a quarter to a third of the biological activity in such a bottom. Different types of the same size show a three times variation in rate of O_2 uptake. A correlation seems to exist between respiration rate and feeding type.

INTRODUCTION

The physiology and the physiological-ecological relationships of the small invertebrate (meiofauna) communities of marine substrates have never been investigated; a first attempt is presented in this paper. A soft-bottom habitat was chosen for analysis in view of the increased occupation in recent years with this type of environment as an ecosystem (Smidt 1951, Sanders 1956, 1960, Teal 1959a, Pomeroy 1959, Wieser 1960). The investigation was confined to the nematodes which in soft-bottom substrates represent by far the most abundant group of small invertebrates (Wieser 1960).

MATERIALS AND METHODS

Quantitative samples were taken by means of plastic tubes of 10 and 1 cm^2 cross section pushed into the mud by hand. In the latter case the whole sample was sorted out under the microscope, in the former only a fraction of it. For the counting of the nematodes a "Bogorov tray," which is commonly employed for the counting of plankton, was found useful.

For experimental purposes samples were taken to the laboratory and kept as close as possible to the temperature which prevailed in the habitat at collecting time by using a cold room or refrigerator when necessary. The samples were collected between October, 1958, and June, 1959, when the water temperature varied from –1.5°C to 18°C.

Volume and weight determinations of nematodes were carried out as described by Wieser (1960).

Oxidation-reduction potential profiles were made by pushing a platinum electrode down into the core. The calomel reference made contact with the sediment at the surface.

Latent oxygen combining capacity of the sediment at different depths was measured by extruding 1 ml of the sediment into a bottle containing aerated sea water. This was immediately sealed with an oxygen electrode (Kanwisher 1959) and the time course of disappearance of the dissolved oxygen was followed on a recorder.

The anaerobic survival of nematodes was studied in Thunberg tubes that were flushed more than 20 times with tank nitrogen, then closed and left in a refrigerator for varying periods of time.

Determinations of oxygen consumption were made by the cartesian diver method as described by Holter and Linderstrøm-Lang (1943) and by Zeuthen (1947). The divers had a volume ranging from 6.5 to 37.4 μl and volume changes could be read to 0.001 μl/hr in the smallest and 0.006 μl/hr in the largest diver. The divers were filled with sea water and the nematode(s) transferred by means of a fine steel needle (Kerr pulp files no. 1). After the nematode(s) had sunk to the bottom of the diver, the superfluous water was sucked out with a fine pipette. Consequently, the volume of the water drop was

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[2] Contr. No. 1167 from the Woods Hole Oceanographic Institution.

not exactly controlled. The neck of the diver was closed with a KOH (conc.) and an oil seal, but no special flotation medium seal was put in. The volume of the gas space was determined by weighing the diver on a torsion balance with the water drop and the seals in their place. The experiments were performed either on single individuals or on batches of up to 5 equal-sized specimens. The experimental temperature was usually 20°C, in some cases 21 and 22°C, all ± 0.01°C. All values were corrected for 20°C, assuming the temperature/metabolism relationship of Krogh's standard curve (Krogh 1941; *cf.* Overgaard Nielsen 1949). The animals used had been kept in the laboratory for varying amounts of time, mostly 1 to 5 days, but sometimes as much as 16 days. Food was available in the form of mud and detritus from the original sample. Thermal adjustment to the experimental temperature was short, not more than a few hours, which, in view of the small size of the animals and the absence of temperature compensation in their metabolism (see below), should be sufficient. This is in agreement with the findings of Overgaard Nielsen (1949) in terrestric nematodes.

HABITAT

The habitat investigated was the sandy mud at the edge of a small *Spartina* marsh on Penzance Point, near Woods Hole, Massachusetts. The sediment actually covers old portions of the Spartina flat. From about 2 cm downwards dead roots of *Spartina alterniflora* are mixed into the sediment until they form a dense mat through which the plastic tube can be pushed only with difficulty. The sediment is sandy with a high proportion of silt and mud. Its appearance in a core is dark grey to black, overlain by a lighter and fluffier layer of detritus of varying thickness. All the samples were taken from a very small area which is covered by water of normal oceanic salinity at high tide and uncovered at low tide.

The general picture of the bottom sediment as a habitat is as follows. The interstitial water is trapped between the sediment particles and so supplies very little oxygen by its movement. Some oxygen is supplied by diffusion from the surface through this water phase. But the *in situ* biological demand is greater than this supply below about 1 cm and the environment becomes anaerobic. The redox potential drops very quickly at this level to values as low as –400 mv. No oxygen could be detected by probing with an oxygen electrode below 1 cm. Any doubt about the completeness of the anaerobicity inferred by the redox potential is removed by the rapid rate at which the sediment combines with oxygen when placed in aerated sea water. This is some thousand times faster than the oxygen consumption at the surface of an undisturbed core.

DISTRIBUTION OF NEMATODES

The population density of the nematode fauna at the collecting site varies from 1.4 to 2.1 × $10^6/m^2$. A list of the species found (Table 1) suggests that the distribution of several forms is patchy. Some species may be present in fall, but absent (or not detectable) in spring. While this cannot be verified for the less common species, it is certain for *Metoncholaimus pristiurus*, one of the most abundant species in the two November samples but entirely absent in the June sample. Moreover, repeated attempts to find this species for the measurement of oxygen consumption failed after about the middle of December. From that time on, *M. pristiurus* seems to be replaced by its close relative, *Oncholaimus campylocercoides*.

The data on the vertical distribution show that the dominant species are also those that penetrate most deeply into the mud. The decrease in number of specimens with increasing depth need not necessarily reflect an actual impoverization of the fauna but may be due to the reduction of available space since with increasing depth there is an enormous increase in the amount of dead *Spartina* roots per volume of mud. For example in the June sample, which did not contain any nematodes below 4 cm, the 0–2 cm layer contained no roots while in the 2–4 cm and the 4–6 cm layers the filter dried weight of *Spartina* roots amounted to 263 mg/cm^2 and 500 mg/cm^2 respectively.

TABLE 1. *Species and weight composition of nematode fauna in Penzance Marsh, Woods Hole*

Sample no.	Species composition (% of population)						Biomass (% wt)	
	Pen-1	Pen-2			Pen-12		Pen-1	Pen-12
Vertical sections (cm)		0–2	2–4	4–6	0–2	2–4		
Metoncholaimus pristiurus	38.3	3.9	1.8	12.5			57.3	
Sabatiera vulgaris	29.9	13.3	30.9	37.5	12.8	4.8	22.3	14.4
Spirina parasitifera	16.5	27.6	32.7		25.6	71.5	9.1	37.0
Halichoanolaimus longicaudatus	1.5	1.3	14.5				0.2	
Tripyloides gracilis	3.1	15.8					4.9	
Metalinhomoeus typicus	0.8	1.3	7.3				0.3	
Pareurystomina flagellicaudata	0.4	1.3					0.2	
Terschellingia n. sp.	1.1	1.8	1.8	37.5	7.7		0.3	1.6
Theristus setosus	0.8	5.3			5.1		0.6	4.7
Oncholaimus campylocercoides	0.4		1.8		9.0	14.3	0.2	16.4
Anticoma litoris	3.8				21.8		3.1	14.4
Terschellingia longicauda	1.1						0.2	
Theristus frictor	1.1						0.3	
Nudora lineata	0.8						0.3	
Spilophorella paradoxa		2.0	1.8					
Halalaimus pachydermatus		2.0	1.8					
Chromadora axi		3.3						
Monoposthia costata		1.3						
Desmolaimus fennicus		1.3						
Prochromadorella neapolitana		1.3						
Pareurystomina typicum		0.6						
Dermatolaimus elegans			1.8					
Hypodontolaimus carinatus		9.2			1.3			1.0
Paracanthonchus caecus		3.9			6.4			2.9
Hypodontolaimus balticus		2.6			1.3			1.0
Axonolaimus spinosus		0.6			1.3			0.2
Neochromadora poecilosoma					6.4			5.1
Odontophora papusi					1.3			0.4
Chromadorina germanica						4.8		0.4
Specimens examined	261	152	55	8	78	21		
Specimens/cm^2	213	71	68	5	170	24		
Specimens/cm^2 total	213		144		194			
Other meiofauna groups	4		5					
Biomass (wet wt g/m^2)							18.4	8.7
Collecting date	11/4/58	11/11/58			6/26/59			
Water temperature °C	8.5	9.0			18.0			

Moore (1931), Rees (1940), Mare (1942), Bougis (1946), and Smidt (1951) all agree that most nematodes can be found in the upper 4 cm of the mud, that they reach further down than the other groups of metazoans, and that the lower limit of the vertical penetration of marine nematodes into the mud lies around 8 cm. Within the limits of the present investigation these conclusions are supported by the data summarized in Table 1.

ANAEROBIC SURVIVAL

In view of the low E_h and the latent oxygen combining capacity below 1 cm in the mud it seems clear that all species we found must be able to tolerate highly reduced conditions. Moore (1931) found living nematodes in mud samples kept for a month in a reduced state in a rubber stoppered bottle. We have checked our material by putting 5 samples of mud together with a small amount of water into 5 Thunberg tubes, flushing the

TABLE 2. *Anaerobic survival of Penzance nematodes*

Sample no.	1, 2	3	4, 5
Number of days at reduced conditions	10–11	21	50–60
E_h volts at surface of mud	−.01 to −.04	?	−.06 to −.16
Anticoma litoris	→	→	→
Stenolaimus marioni	→	→	→
Longicyatholaimus quadriseta	→	→	→
Prochromadorella neapolitana	→	→	→
Sabatiera vulgaris	→	→	→
Sabatiera cupida	→	→	→
Odontophora papusi	→	→	→
Steineria n. sp.	→	→	→
Nudora lineata	→	→	
Hyalacanthion n. sp.	→	→	
Chromaspirina ciliata	→	→	
Chromaspirina n. sp.	→	→	
Spilophorella paradoxa	→	→	
Monoposthia duodecimalata	→	→	
Desmodora cephalata	→	→	
Paracanthonchus caecus	→	→	
Tripyloides gracilis	→		
Spirina parasitifera	→		
Ascolaimus elongatus	→		
Chromadora axi	→		
Oncholaimus campylocercoides	→		
Theristus setosus	→		
Oncholaimus paralangrunensis	→		
Monoposthia costata	→		
Hypodontolaimus carinatus	→		
Neochromadora poecilosoma	→		
Axonolaimus spinosus	→		

latter with nitrogen and storing them in a refrigerator at about 7°C. Before closing, some methylene blue was added to each Thunberg tube. The tubes were opened after a period from 10 to 60 days, the redox potentials at the surface of the mud were read and representative samples of the living nematodes were picked out under the microscope. The list of the species found (Table 2) again reflects the patchy distribution of some of the species. For this reason the absence of certain species in the most highly reduced samples, 4 and 5, cannot be taken as proof that these species would not survive extreme conditions. Since our negative E_h values indicate the absence of dissolved oxygen, it is safe to assume that all nematode species listed in Table 2 are able to live anaerobically for some time. It might be added that in samples 4 and 5 the mud was completely black and smelled of H_2S. In all samples the methylene blue was decolorized and turned blue again after exposure to air.

RESPIRATION

Despite the fact that all mud-inhabiting nematodes must be able to live anaerobically for some time, they can be kept for long periods in a well-aerated medium. Since the water overlying the Penzance Point mud at high tide is saturated with oxygen and stirs to a varying extent the top layer of the substrate, there must exist at times a mud-water interface in which the oxygen content falls from saturation to near zero and in which, consequently, nematodes have the opportunity of using oxygen for their metabolism. The thickness of this layer is probably never greater than 1 cm, but this upper centimeter is by far the most densely populated of all layers in the mud (Smidt 1951). This means that in large portions of the meiofauna of marine muds, periods of aerobic and anaerobic metabolism might alternate with each other. We can thus justify oxygen consumption determinations of metabolism in these mud-inhabiting animals. Such data for a number of the Penzance species is summarized in Table 3 and Figure 1. It was possible to measure representatives of most of the abundant and moderately abundant species listed in Table 1.

Although a great number of species belong to the size group from 2 to 8 μg, there is a considerable spread in the oxygen consumption, ranging from an average of 370 $mm^3/g/hr$ in *Spirina parasitifera* to 1,800 $mm^3/g/hr$ in *Axonolaimus spinosus*. This will be discussed below.

Comparison of the oxygen consumption of animals collected in winter and in summer or fall gives no indication that the species examined are able to compensate their metabolism for temperature changes. This means that in winter the metabolism of the whole nematode fauna will be very much reduced, which is in agreement with the findings by Wieser and Kanwisher (1960) for *Enoplus communis* and by Overgaard Nielsen (1949) for terrestric nematodes.

The range of variability in respiration rate

TABLE 3. *Oxygen consumption of Penzance nematodes, range and mean in parentheses*

	mm^3 O_2/g/hr at 20°C	No. of determinations	Wet wt (μg)
Axonolaimus spinosus	1070–2580 (1800)	3	1.5– 2.9 (2.0)
Oncholaimus paralangrunensis	1210–1640 (1410)	5	3.4– 7.2 (5.7)
Bathylaimus kanwisheri	1300	1	5.0
Tripyloides gracilis	940–1860 (1285)	10	4.5– 8.6 (6.0)
Oncholaimus campylocercoides	860–1260 (1100)	6	11.0–22.0 (16.5)
Metoncholaimus pristiurus	610–1350 (918)	13	17.0–26.0 (21.2)
Theristus setosus	410–1100 (741)	16	5.0– 8.4 (6.5)
Odontophora papusi	660– 920 (726)	5	2.2– 5.0 (4.2)
Bolbella tenuidens	485– 815 (650)	2	16.0–26.0 (21.0)
Sabatiera vulgaris + *S. cupida*	455– 765 (605)	6	3.4–11.0 (7.3)
Monoposthia costata / *Nudora lineata*	445– 760 (590)	7	2.6– 3.9 (3.3)
Paracanthonchus caecus	356– 790 (563)	7	3.2– 5.5 (4.4)
Anticoma litoris	400– 625 (488)	6	7.0– 9.6 (8.3)
Terschellingia sp.	450	1	3.0
Spirina parasitifera	290– 540 (367)	6	4.1– 7.0 (5.9)
Halichoanolaimus longicauda	224– 510 (346)	4	21.0–57.0 (36.8)

lies around 100% in most species. While we believe that even under completely homogeneous experimental conditions the oxygen consumption of any species of invertebrates might vary by about 100%, the following possible sources of experimental variability should be mentioned. The weight determinations are based on the measurement of length and width of the animals and are therefore bound to introduce errors of as much as 10%. The animals were not starved before the experiments and thus might have been in different states of nutrition. However, Overgaard Nielsen (1949) has found that starving up to 7 days has no effect on the oxygen consumption of terrestric nematodes. The absence of an extra flotation medium seal might have allowed the flotation medium to penetrate at varying lengths into the neck of the diver, but the uncontrolled variability in the volume of the gas space so caused should not have exceeded 10%.

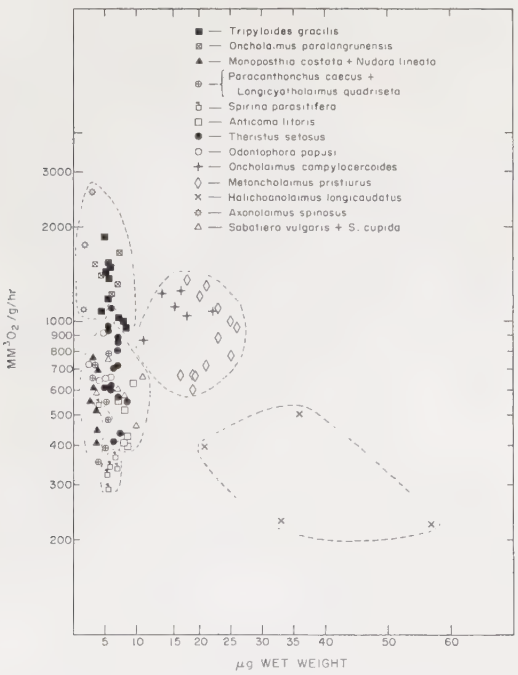

FIG. 1. Oxygen consumption of the more abundant species of nematodes from Penzance Point marsh near Woods Hole, Mass. Each convention denotes one experiment.

DISCUSSION

The density of the nematode fauna in the littoral mud of Penzance Point varies from 1.4 to 2.1 × $10^6/m^2$. This may be compared with a density from 2.8 × $10^5/m^2$ to 1.8 × $10^6/m^2$ in the offshore muds of Buzzards Bay in the same area (Wieser 1960). Smidt (1951) found about 1.0 × $10^6/m^2$ in the intertidal mud of the Danish Wadden Sea, but Rees (1940) about 10 times as many in the intertidal of the Bristol Channel. Thus it appears that the differences in population density between various intertidal areas are greater than those that might be encountered

between the intertidal and the shallow sublittoral of the same area.

The nematode biomass can be estimated from volume determinations as used by Overgaard Nielsen (1949) and by Wieser (1960). This has been done for samples Pen-1 and Pen-12, using an average value for all adults of one species and assuming that the average weight of the juveniles was half that of the adults. This produces wet weights of 18.4 g/m^2 for the November sample (Pen-1), and 8.7 g/m^2 for the June sample (Pen-12). The smaller value for the June sample may be significant since at this time of year the large species *Metoncholaimus pristiurus* which dominated the November sample could not be found. Values of 8.7 g/m^2 and 18.4 g/m^2 indicate that the nematode biomass in the Penzance Point mud is about 10 times richer than the soft-bottom habitats of the shallow sublittoral. The corresponding figures are 0.4–2.5 g/m^2 for Buzzards Bay (12–30 m deep; Wieser 1960) and 1.15 g/m^2 for Plymouth Sound, England (45 m deep; Mare 1942). On the other hand, there is close agreement with the values given for certain types of terrestric habitats. Overgaard Nielsen (1949) found in Danish grass fields the biomass of the nematodes to vary between 6 and 17.8 g/m^2.

Our measurements of Q_{O_2} on most of the abundant nematode species permit the calculation of the total respiration of the nematode fauna per unit of surface area. As has been pointed out, the mud below 1 cm is always highly reduced and yet contains a considerable number of nematodes. Since our measurements were made with air in the cartesian diver, such a use of the figures assumes that nematodes have the same energy requirements whether living aerobically or anaerobically. The only indication that this is so comes from our repeated observations that the nematodes in question show identical speed and type of movement in an aerated dish and in a Thunberg tube with a highly reduced substrate.

The oxygen consumption of the nematode populations in samples Pen-1 and Pen-12 can be calculated, using the average Q_{O_2} values listed in Table 3 and the weight distribution given in Table 1. There are only few and relatively rare species of which the oxygen consumption is not known and these are assigned Q_{O_2} values of closely related species. In such a manner a total oxygen consumption of 13.9 cc/m^2/hr for Pen-1 and of 5.1 cc/m^2/hr for Pen-12 is found for a temperature of 20°C. In calculating these values the juveniles of each species were assumed to possess the same respiration rate as the adults. This assumption is certainly incorrect (see Overgaard Nielsen 1949, Wieser and Kanwisher 1960) but the error introduced by it is small. The total oxygen consumption of the nematode fauna of Danish grass fields measured at 16°C by Overgaard Nielsen varied between 5.8 and 17.3 cc/m^2/hr and thus agrees well with the data from the Penzance salt marsh.

Oxygen consumption per unit area of the bottom was determined as a measure of the energy utilization of the entire bottom community. Cores taken in plastic tubes were layered with sea water. Mineral oil was added on top to prevent gas exchange with the air. The sea water was kept mixed by stirring with a wire loop. The decrease in dissolved oxygen with time was followed by determinations made on 1-ml samples withdrawn by syringe. In November (Pen-1) the bottom consumption averaged 36 cc/m^2/hr while the spring determinations (Pen-12) gave a value of 26 cc/m^2/hr. Thus the nematode fauna appears to account for 25 to 33% of the biological activity in the bottom. We have estimated that the macrofauna respiration accounts for 10 to 15% additional of the bottom total. The remainder, more than half, can reasonably be allocated to the smaller forms, bacteria and protozoa. It may be that the highly reduced conditions of the bottom sediments tend to eliminate the larger forms and so produce an opportunity for the biochemically more ingenious bacteria to take over.

Anaerobic processes yield only about 10% of the energy that could be derived by complete oxidation of a food (Brand 1946). Thus the nematodes would have partially to digest a larger quantity of food if an energy requirement equal to that in air has to be

satisfied. Using the dominant species of the November samples, *Metoncholaimus pristiurus*, the following calculation can be made. The average weight of an animal is 20 μg and it consumes about 1,000 m^3 O_2/g/hr at 20°C, or .02 m^3 O_2/hr/animal. Since the consumption of one liter of oxygen corresponds to the combustion of 1.34 g of carbohydrate, one animal in the presence of oxygen used about .029 μg of carbohydrate per hour which, according to the assumption made above, corresponds to about .29 μg of carbohydrate per hour under anaerobic conditions. The intestine of *M. pristiurus* measures on the average, 450 × 50 μ which corresponds to a volume of .00088 mm^3. If the specific gravity of the Penzance Point mud were only slightly higher than 1 (which is certainly too low), one intestine full of mud weighs about 1 μg. Supposing the total content of the intestine were to consist of digestible material with the caloric value of carbohydrate, the nematode could live on it for three hours under anaerobic conditions if it spent as much energy as it does under experimental conditions in the presence of oxygen at 20°C. If only 10% of the mud consisted of digestible material, one filling of the intestine would last for not more than 18 min.

Such a rapid rate makes our measured values of oxygen consumption less convincing. It is likely that in an undisturbed natural substrate, the animal would spend less energy than it would in a drop of water at the bottom of a cartesian diver. However, it is not likely that the experimental figures differ from the values to be expected in nature by, say, 500%. Also the possibility should be considered that nematodes may not, after all, spend as much energy under anaerobic conditions as they do in the presence of oxygen. Either case would make the nematodes energetically less important in the community than we have estimated.

The large range of variation in the respiration rate of nematode species (Fig. 1) is difficult to reconcile with the assumption made by several authors (Müller 1943, Krüger 1952, Bertalanffy 1957, and others) that within a taxonomic group interspecific differences in respiration rate can be sufficiently explained by differences in size (weight or surface) of the species concerned. The range of variation from 370 to 1,800 mm^3 O_2/g/hr in species that differ only little in weight and not at all in surface/volume ratio (see Wieser and Kanwisher 1960) seems to point definitely toward basic metabolic differences in these species. Similar large differences between related species of the same size group were found by Schwartzkopff and Wesemeier (1959) and by Wesemeier (1960) in mollusks.

We may rule out the possibility that different species are differentially harmed by the presence of oxygen since, as already mentioned, all species can be kept alive for long periods in an oxygenated medium. On the other hand, there is a clear correlation between oxygen consumption and degree of activity of the species. The species with respiration rates between 300 and 500 mm^3/g/hr are definitely more sluggish than those with respiration rates of 700 mm^3/g/hr and more. The species with respiration rates of greater than 1,200 mm^3/g/hr are almost constantly active in a dish, either swimming with whip-like motions of the whole body (*Axonolaimus spinosus*, *Oncholaimus paralangrunensis*) or continuously coiling and uncoiling (*Tripyloides gracilis*, *Bathylaimus kanwisheri*). On the other hand, *Spirina parasitifera* and *Anticoma litoris* can often be observed lying motionless in a rigid position at the bottom of the dish or coiled around shreds of algae or sand grains.

Different levels of oxygen consumption may also be explained by the existence of a correlation between respiration rate and feeding type. If the shape of the buccal cavity is pictured alongside a list of species arranged according to levels of oxygen consumption (Fig. 2) it is found that large buccal cavities are typical of species with high oxygen consumption, small buccal cavities of species with low oxygen consumption. The only exception to this rule is the largest species found, *Halichoanolaimus longicaudatus*. The three species with an average oxygen consumption between 350 and 500 mm^3 O_2/g/hr belong to what Wieser (1953) has called group 1-A, in which the

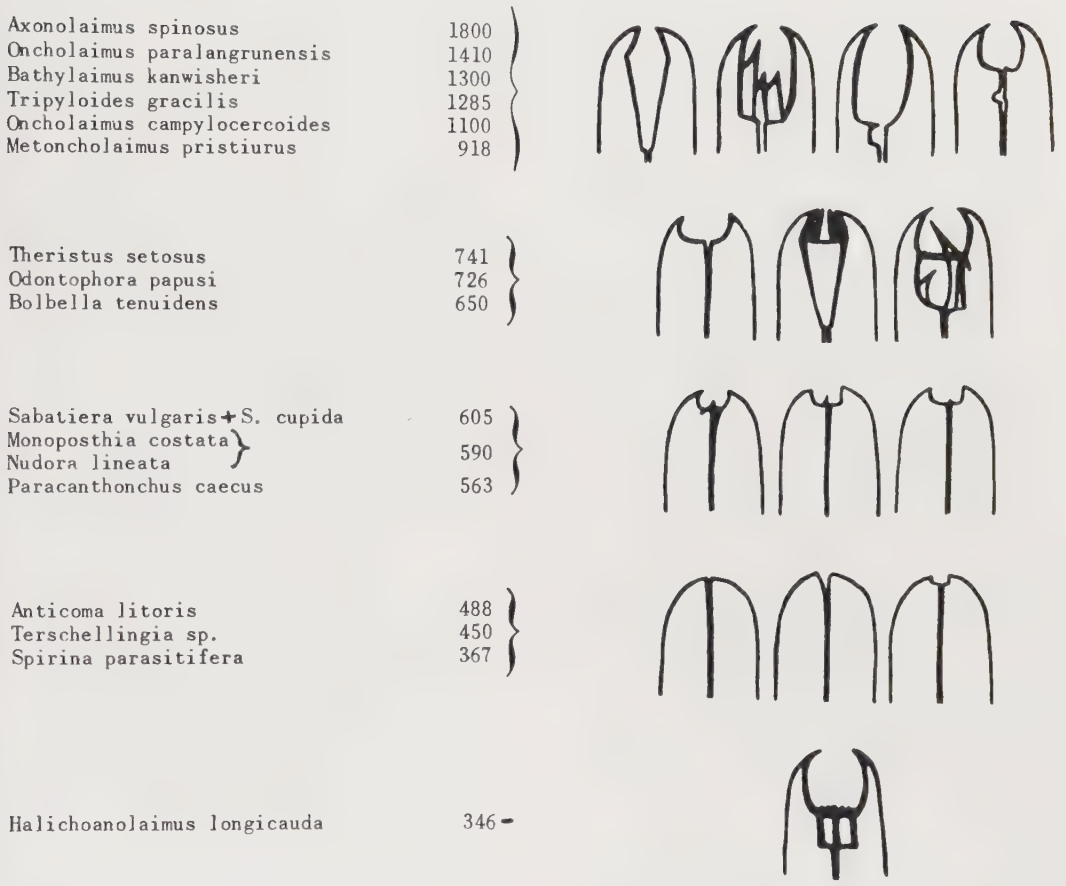

FIG. 2. Average respiration rate, in mm^3 O_2/g/hr, of nematode species from Penzance Point marsh near Woods Hole, Mass., together with outline drawings of anterior end of species studied in order to show relationship between respiration rate and shape of buccal cavity.

buccal cavity is either absent or very small (in the above-mentioned paper the genus *Spirina* was erroneously referred to group 2-A). The species with an average oxygen consumption of approximately 600 mm^3 O_2/g/hr belong to group 2-A which is characterized by a medium-sized buccal cavity and the possession of small teeth. The remaining species all of which have respiration rates above 650 mm^3 O_2/g/hr are in groups 1-B and 2-B which possess large buccal cavities, either armed with teeth or unarmed.

The most plausible interpretation of this relationship is that the different types of buccal cavities represent different feeding types and that the amount of oxygen required to sustain the metabolic and behavioral functions of these feeding types is also different; for example, the species with large buccal cavities may be non-selective deposit feeders and ingest a large amount of material of which they use only a fraction; while the species with small buccal cavities may be selective deposit or epigrowth feeders in which the ratio of digested to ingested material is higher. Obviously, the non-selective feeders would have to roam about more widely, and so be more active than the selective feeders. This is in agreement with observations on the general activity in the species concerned. The exceptional position of *Halichoanolaimus longicaudatus* may be due to a mode of feeding different from that of the other spe-

cies with large buccal cavities. It may be pointed out that the genus *Halichoanolaimus* (together with the genus *Sphaerolaimus* which is not represented in the material) contains species in which predatory feeding habits are better established than in any other species of marine nematodes (Ditlevsen 1919, 1921, Allgén 1939, Wieser 1960).

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BOTTOM SAMPLING AND ENVIRONMENTAL NICHES[1]

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ABSTRACT

Sampling different environments at the bottom level in marine waters indicates that areas of small extent may have very different biotas, both as to component species, and as to total numbers. In fine particle (mud) bottoms, the algae and protozoa are concentrated in the 2 to 5-mm mud-water interface. In sand at the tide line, they are concentrated at somewhat deeper levels. If the bottom is anaerobic the biota is characterized by sulfur bacteria, certain colorless euglenids and ciliates. In aerobic bottom areas, this work indicates a smaller, less extensive biota. The amount of sampling however, was not sufficient to make this a conclusion.

In the mud-water interface of 5 aquaria where H_2S reached the surface in small patches, there was a larger and more varied population than in non-sulfurous mud a few centimeters away. It is apparent that microclimatic factors are responsible for large biotic differences within short linear distances, and that one should sample benthic populations in an undisturbed mud-water interface. Either a large area should be sampled, or many core samples should be taken, the latter method being preferable.

INTRODUCTION

A prime consideration in assaying the population of an environmental niche is that of securing representative samples. This becomes increasingly difficult in securing bottom sediment samples where one cannot see the bottom, or where there may be differences in the composition of the bottom, which are not apparent to the eye, because of underlying differences. If one is sampling for large organisms, shellfish, for example, the difficulties become less, because it is easier to sample large areas. But if one is sampling a cross section of the microscopic bottom organisms, the difficulties are much greater. Organisms there may follow holophytic modes of existence, where there is light, or holozoic, or saprozoic modes. Their oxygen demands and their responses to physical substrate vary. Since considerable difference of all these and other environmental factors is possible within very short distances, the question of what constitutes a representative sample may well be raised.

Analysis of core samples from the ocean bottom at Woods Hole, Massachusetts, indicated that cores often brought up almost undisturbed sections from above the bottom to a considerable depth into the mud. Use of a long pipette with a 1.5-mm opening permitted withdrawal of a very small sample for direct examination. Since these cores were little more than an inch in diameter, they could be studied intensively. A considerable variation was noted in their biota, in accord with the above statements.

METHODS

In the summer of 1960, there were five wooden boxes, each about 12 in. deep and 12×18 in. along their sides, filled with bottom soil from an estuary, in use at the Narragansett Marine Laboratory, University of Rhode Island. They were standing on a concrete table and water from the Bay flowed over them continuously. Although used by another worker for other purposes they were virtually undisturbed. The water was about one inch deep over the mud-water interface and there was little or no disturbance of the mud surface. Along the wooden sides at 9 different locations, were white patches of Beggiatoales, sulfur bacteria. Nine points within the sulfur bacteria colonies and 10 points elsewhere on the surface were sampled intensively for a period of 5 weeks. Only the mud-water interface, *i.e.*, the top 2–5 mm, was examined, but algae, protozoa, and certain sulfur bacteria were identified, and their relative abundance was noted. Special attention was paid to the dominant organ-

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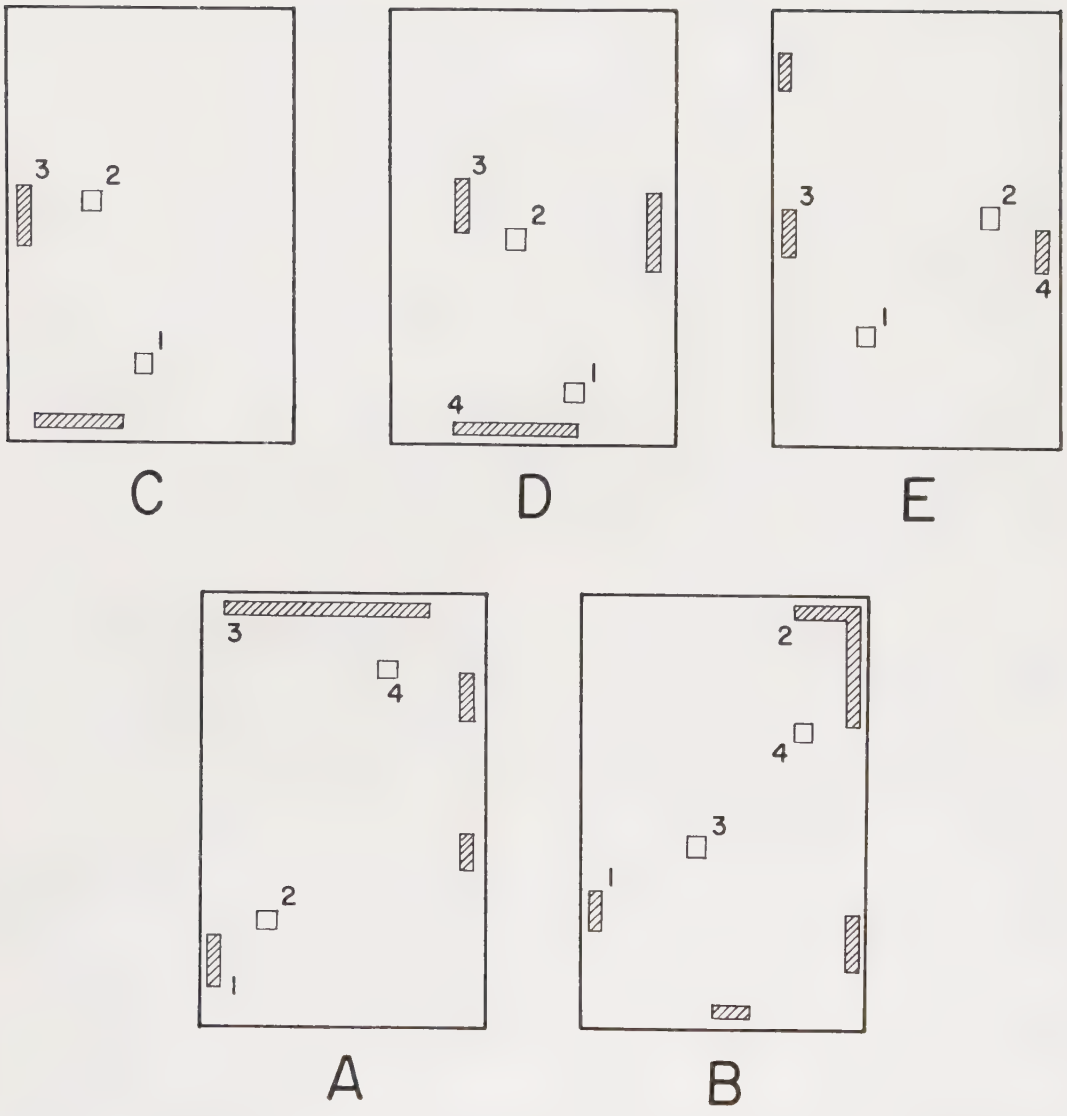

FIG. 1. *Sampling locations in the five aquaria.* The ten white squares represent non-sulfur bacteria locations. The crosshatched areas, only nine of which were sampled, represent patches of sulfur bacteria.

isms at each point and to whether they persisted for the duration of the study.

Nematodes, tardigrades, copepods, rotifers and annelids were noted, but other metazoa occurred so sparingly in the samples that no particular significance could be attached to them. Nematodes were always abundant, but no attempt was made to determine species. It is taken for granted that they play a large part in the turnover of organic matter at the surface or just below it.

Figure 1 shows the location of the sampling points in the boxes. It will be noted that the points were often only 2–3 in. apart. In practically all the locations, there was a fine, flocculent mud; light gray or gray-brown where there were no sulfur bacteria, black beneath the coating of sulfur bacteria. Time did not allow any chemical work, but the external conditions of light, temperature, flow of water, and other such factors remained fairly constant. Under such condi-

tions, it might have been assumed that a fairly stable and uniform biota would develop.

Actually two differing biotas were found in these aquaria. One of these, the most abundant, occurred in the *Beggiatoa* patches; the other, much more limited in numbers and kinds, occurred in the mud somewhat distant from these patches. Some species which seem to be ubiquitous occurred anywhere but generally in small numbers.

Two other environments were sampled to some extent during the summer, and because they contained sulfides and hydrogen sulfide, their organisms are compared to those of the wooden aquaria. One environment was at a depth of 4–6 in. in the sand of the beach between low and high tide mark. The method of sampling was simply to excavate a hole, up to 18 in. across. As water gradually seeped in, it was agitated repeatedly, and then a liter or less of the silty water was dipped up. The sand settled in a matter of seconds, and the supernatant water contained a representative population. The water when freshly dipped smelled faintly but distinctly of H_2S.

The other samples were the mud-water interface of cores secured from Charleston Pond, Green Pond, and deep holes far up in Narrow River. These were distinctly sulfurous, especially those from Narrow River. The river samples possessed a deep upper layer of flocculent brown mud and were almost barren. All are salt water.

There were 9 sampling points in the sulfur bacteria patches of the aquaria, 10 from non-sulfur bacteria locations, 4 sand beach sampling points, and 15 core samples. The aquarium samples were examined about 4 times each, the sand samples about 4 times each, the cores but once each. In all, about 100 examinations were made. Most of the emphasis was simply on listing organisms. Except for some generalizations, the work reported here is primarily qualitative.

RESULTS

Since the basis of separation into environments for the aquaria was the presence or absence of patches of sulfur bacteria, all such identified bacteria were listed. The list is shown in Table 1. It includes Beggiatoales, two of the Thiobacteriaceae, and one of the Thiorhodaceae. Sulfur purple bacteria had a random distribution, when present. Considering the wide tolerance of environmental factors by the colorless, sulfur-containing bacteria Table 1 is short. The genus *Thiothrix*, for example, was not found at all. Nevertheless, the aquaria had a wide and constant representation of these forms. It is worth noting that 44 occurrences were in the 9 sulfur patches, and only 9 in the 10 sampling points outside the sulfurous patches. Compared to these 9 areas, the distribution elsewhere indicates radical differences in nearby environments, as well as in the sand and pond situations. Comments on the nature of the differences will come later, but it might be stated that none of these three environments would seem to provide the physical types of attachments found where *Thiothrix* is common.

Algae, except for diatoms, were sparse in all types of the locations surveyed. Bluegreens, Volvocales, Chlorophyceae, Chrysophyceae, and Cryptophyceae comprised only 16 species. These were found 15 times in the aquaria, 23 times in the sand, and 34 times in the ponds. Of these 72 occurrences, 40 were due to Cryptophyceae. But there were never large numbers of any single species.

Chloromonads included 4 species, one

TABLE 1. *Occurrence of certain colorless sulfur bacteria in sampling stations at the Narragansett Marine Laboratory, summer of 1960*

Species	Aquaria	Occurrences in sand	Ponds, including Pettaquamscutt River
1. *Achromatium oxaliferum*	4	5	1
2. *Beggiatoa alba*	10	6	3
3. *B. arachnoidea*	8	6	2
4. *B. gigantea*	1		
5. *B. leptomitiformis*	5	1	
6. *B. minima*	1		1
7. *B. mirabilis*	10	2	1
8. *Vitreoscilla beggiatoides*	1		
9. *Thiovulum majus*	10		4
10. *Thiospira bipunctata*	3		
11. *Thiospirillum jenense*			1
Totals	53	20	13

definitely new, another possibly so. The abundant one occurred 7 times in the sand. *Thaumatomastix* occurred 3 times in the sand, once in the aquaria. *Trentonia*, common in Warm Mineral Spring, Florida, also occurred in a single Charleston Pond sample. Warm Mineral Spring is about half sea water, and salinity is lowered in Charleston Pond. It is quite evident that sampling, for members of this group, would be useless, except at a depth of a few inches within sand. It almost appears that this group may provide indicator organisms; to obtain *Gonyostomum*, one looks at acid water from a cedar or cypress bog or pond; *Trentonia* is restricted in habitat; and some genera now appear common within marine sand.

Euglenophyceae

Forty-three Euglenophyceae were found in these studies. This includes those to which some definite status could be given because of continuity of observation, or recurrence. There were other additional probable members. At least 3 new species were studied sufficiently to be described in the literature (separate paper, in preparation) but when time permits, similar habitats will be investigated for others that are probably new.

Almost all of these euglenids, as might be expected, are colorless. Only 6 records were made of green members, but except for *Eutreptia*, green members tend to be sparse in salt water, and as a benthic component. Table 2 indicates a very general colonization of the mud-water interface, and of the first few inches of wet sand between tide marks by the group. Some, such as *Anisonema ovale* and *Notosolenus apocamptus* tend to be ubiquitous; others, such as the organisms tentatively called *Notosolenus spinosus* (found thus far only at this location) and *Sphenomonas elongata* (from both Rhode Island, and La Jolla, Calif.), tend to be sand dwellers. Considering their size, the fact that most of them are saprozoic in nutrition, and the observation that they work over a clump of organic matter very thoroughly, it seems they must be very important in the cycle of organic matter at the bottom. It is evident also that they are quite tolerant of H_2S or sulfides. This could be guessed from records of their occurrence elsewhere, but in the aquaria they occurred 43 times in the patches of sulfur bacteria, and 15 times in the non-sulfur patches. This tolerance of sulfur might well mean an important role of euglenids in the sulfur cycle itself.

TABLE 2. *Occurrence of Euglenophyceae in sampling stations at the Narragansett Marine Laboratory, summer of 1960*

	Number occurrences		
	Aquaria	Sand	Ponds
Anisonema dorsalis p.n.	1	1	
A. emarginatum	2	2	2
A. lineatum p.n.	1	1	
A. minuta p.n.	3	6	1
A. ovale	9	11	4
A. pusillum	6	6	3
A. truncatum p.n.			1
Anisonema sp.	1		
Calkinsia truncatum			1
Distigma proteus	1	1	
D. striato-granulatum	2	1	
Entosiphon obliquum		1	2
E. polyaulax	1	1	
E. sulcatum	4		
Entosiphon sp.			1
Euglena polymorpha			2
Euglena sp., colorless		1	
Euglena sp., green	1		1
Eutreptia lanowii			1
Metanema variable		1	1
Notosolenus apocamptus	8	3	5
N. pusillus p.n.	1		
N. spinosus p.n.		8	
Peranema trichophorum		3	4
Peranemopsis striata		1	
Petalomonas angusta	2	2	3
P. dorsalis		2	1
P. globosa p.n.		2	
P. inflexa			1
P. mediocanellata	1		1
P. pusilla		2	
Petalomonas sp.	1		1
Pleotia tricarinata p.n.	1		
Pl. vitrea	2	2	2
Sphenomonas elongata p.n.	3	10	1
S. angusta	1		
S. quadrangularis			1
S. teres	1		
Sphenomonas sp.			2
Trachelomonas obovata			1
Triangulomonas rigida			1
Urceolus sabulosus	4	3	2
U. macromastix			1
Scytomonas pusilla	1		
Calkinsia sp.			1
	58	71	48

In the aquaria, the euglenids were found in the first 2–3 mm of the flocculent matter. They occurred not at all in the samples taken below this level. At first, any sampling included a surface (2–3 mm) examination, a 5–10 mm, and a 15 mm depth. So few organisms occurred at the last two depths, that after a while they were only probed at random. Quite evidently, a true picture of the biota would not have been obtained without specifying that the number of organisms in a sample was in relation to a given depth and area. A one-inch sample might hit a patch of sulfur bacteria, but probably not, since they were mostly at the sides. And if it penetrated as much as 15 or 20 mm, the numbers obtained would be small compared to the volume, whereas they might actually be abundant in the thin surface layer where biochemical activity is most intense. It seems necessary to appraise very carefully the area, depth, and variation in makeup of any bottom sample before generalizing concerning its microbiota.

Diatoms

One surprise was the frequent occurrence, in small numbers, of living diatoms at a considerable depth in the coarse sand. Most of the diatoms were neritic species which settle out readily and in the rather coarse sand these active movers could readily move about. Some diatoms also tolerate greatly reduced light for a long period. But quite a few of the active forms were colorless, and it is assumed these are at least facultative, if not obligate saprophytes.

More than 40 species were observed, and careful identification probably would have shown many more. The genera were the usual ones. While occurrence was frequent, numbers were usually small. There were 263 occurrences in the aquaria samplings, 99 in the sand, and 79 in the pond series. Diatoms in the aquaria were distributed at random, irrespective of the H_2S patches.

Dinoflagellates

Only 11 genera of dinoflagellates were recorded, with better than 25 species. *Amphidinium*, *Gymnodinium*, *Hemidinium*, and *Massartia* were abundant, although on two occasions *Thecadinium kofoidi* was numerous in sand samples. The first four genera were represented by small species, most of them saprozoic, and out of 72 occurrences in the aquaria, 53 or 73% were in the sulfur bacteria patches. There were 51 occurrences in the sand, known to contain H_2S, and only 4 in the pond samples. *Massartia glandula* seems to occur at random in mud-water interface samples, but *Amphidinium scissoides*, *A. scissum*, *A. truncatum*, and *Thecadenium kofoidi* are definitely sand dwellers.

Zooflagellates and rhizopods

Only 14 genera, about 25 species, of Zooflagellates were recognized. Without exception, they were small and they were not numerous. Most of them were holozoic types and facultative anaerobes. Numbers encountered indicate a minor role for Zooflagellates in the ecology of the situations studied.

Rhizopods were also few in numbers. About 15 genera were recognized, but there were at least as many genera or species for which no identification could be made. It is believed that many of the small salt-water heliozoa and testate rhizopods are not now classified. The occurrence of the group was scattered, 23 times in aquaria, 31 times in the sand samples. None were specially abundant, but a very small heliozoön, tentatively called *Actinophrys marina* was probably most numerous. It was expected that the group would be much more important in the mud-water interface.

Ciliates

This is the largest group, both in number of species, and in biomass, in the locations investigated. Table 3 shows the genera and species recognized, including some for which provisional names are used, since they are at present considered new. The figure of 117 could probably have been augmented by taking time to list all identifiable species of genera such as *Euplotes* and *Oxytricha*. Nevertheless, it is an impressive list and accords to the ciliates an importance near that of bacteria in the mud-water interface. It might be pointed out that in coarse sand, this

TABLE 3. *Ciliates encountered at sampling locations at the Narragansett Marine Laboratory, Rhode Island, summer of 1960*

	Number of occurrences in			
	Aquaria			
	sulfur patches	non-sulfur patches	Sand	Ponds
1. *Aegyria oliva* (*Hartmanulla entzi*)	3	2		3
2. *Aspidisca hexeris*			3	
3. *A. costa*		2	2	1
4. *A. minuta*	3	1	4	2
5. *Amphisia* (*Keronopsis flavicans*)			1	1
6. *Amphisiella capitata*			2	
7. *Chaetospira remex*		1		
8. *Chaenia gigas*		1	1	
9. *Chilodonella* sp.			1	
10. *Chlamydodon memosyne*	3	1	6	1
11. *Chlamydodon* sp.	1			2
12. *Chaenia teres*	1	1	1	
13. *Cienkowskya mereschowski*		1		
14. *Cinetochilum margaritaceum*				1
15. *C. marina*	5	2	7	2
16. *Coleps hirtus*			8	1
17. *C. popolateyi* p.n.			1	
18. *C. pulcher*	2		6	
19. *Colpoda* sp.		1		
20. *Condylostoma minutus* p.n.			1	
21. *C. patens*	4	1	1	
22. *Condylostoma* sp.				1
23. *Cothurnia* sp.	2	3	1	1
24. *Cyclidium glaucoma*	8	10	10	9
25. *C. saltans* p.n.			1	4
26. *Cyclidium* sp.				6
27. *Dexiotrichoides centralis*				1
28. *Dichilum cuneiforme*			1	
29. *Diophrys appendiculata*	1	3	4	2
30. *Drepanomonas* sp.	1			
31. *Dysteria monostyla*	1	1	1	
32. *Epalxis exigua*	1	1		
33. *Epiclintes ambigua*	1			
34. *E. caudatus* p.n.				1
35. *E. tortuosus* p.n.		1		1
36. *Epiclintes* sp.				
37. *Euplotes harpa*				1
38. *Euplotes* large	1		5	1
39. *Euplotes* minute			4	1
40. *Euplotes* spp.	6		2	3
41. *Frontonia leucas*	2		1	
42. *Gelcia decolor*		1		
43. *G. fossata*		1		
44 *Hemiophrys branchiarum*			1	
45. *Holophrya marina*	4			2
46. *Holosticha kessleri*	2	3		
47. *Holosticha* sp.	1	2	2	
48. *Lacrymaria cucumis*				2
49. *L. olor*	4	3	5	3
50. *Lembus infusionum*			1	
51. *L. pusillus*	1			
52. *Lionotus cygnus*			1	
53. *L. fasciola*			1	1
54. *L. lamella*	1		2	1
55. *Lionotus* sp.	1		6	3
56. *Loxophyllum helus*			1	
57. *L. setigerus*			1	
58. *Mesodinium acarus*			1	
59. *M. cinctum*	1	2	2	
60. *M. pulex*	2	3	8	7
61. *M. rubrum*	2		9	
62. *Metacystis* spp.	3	4	9	
63. *Metopus es*				2
64. *M. verrucosus*				1
65. *M. vestitus*				1
66. *Metopus* sp.				1
67. *Microthorax sulcatus*			1	
68. *Monochilum ovale*				2
69. *Onychaspis* sp.	2		4	
70. *Ophryoglena* sp.		1		
71. *Oxytricha* spp.	8	4	13	3
72. *Parablepharisma pellitus*	3	8		1
73. *Pelodinium reniforme*	1		2	2
74. *Philaster digitiformis*	1	1		
75. *Peritromus californicus*	1			
76. *P. faurei*	3	2		1
77. *Placus luciae*			2	
78. *Pleuronema chrysalis*	4	2	10	
79. *P. pleuricaudatum*				2
80. *Pleuronema* sp.			1	
81. *Prorodon opalescens*	3	1		
82. *Prorodon* sp.	1			4
83. *Protocrucia pigerrima*	11	5	1	
84. *Ptychocylis* sp.	2	1		
85. *Remanella rugosa*	3	1		
86. *Saprodinium dentatum*				2
87. *Saprophilus ovatus*				1
88. *Sondaria vorax*	1			1
89. *Sondaria* spp.				2
90. *Spathidium* spp.	2	2		
91. *Spirostomum teres*	2	3		1
92. *Stephanopogon colpoda*	1		1	
93. *Stichotricha secunda*		1		1
94. *Strobilidium* sp.	2		3	1
95. *Strombidium* spp.	10	2	7	4
96. *Telostoma ferroi*	3		3	3
97. *Tetrahymena* sp.				1
98. *Trachelocerca coluber*	14	11	2	
99. *T. coronata*	1			
100. *Trachelocerca phoenicopterus*			5	3

TABLE 3. *Continued*

	Number of occurrences in			
	Aquaria			
	sulfur patches	non-sulfur patches	Sand	Ponds
101. *Trachelocerca* sp.	1	1		
102. *Trachelostyla pediculiformis*	7	6	7	1
103. *Trichodina pediculus*			1	
104. *Trichopelma torpens*			2	1
105. *Trochilia dubia*			1	
106. *Uroleptus bacillifer* p.n.	2			1
107. *U. mobilis*	1	2		2
108. *U. pisces*	1	1	1	
109. *U. rattulus*	2		1	
110. *Uroleptus* sp.				1
111. *Uronema granulatum*	2			
112. *U. marinum*	9	8	9	
113. *U. pleuricaudatum*				1
114. *Uronychia setigera*	5	4	4	
115. *Uronychia* sp.			3	
116. *Vaginicola* sp.	1	1		
117. *Vorticella* spp.	1	1	1	
Totals	180	121	210	112

interface consists of the silt and non-sand debris at the water level.

There were 180 occurrences of ciliates in the sulfur bacteria patches of the aquaria, as contrasted with 121 occurrences in the non-sulfurous areas. This is not easily explained, but many of these ciliates definitely ingest certain sulfur bacteria. Certainly there is a strong indication here that the sulfur cycle in nature merits a very close look, particularly with regard to its energy relationships. There were no striking differences as to ciliates occurring exclusively in one situation or the other, so apparently they lived under both microclimatic conditions, but more frequently in the one containing H_2S. This conclusion is furthered by noting that the number of occurrences in the sand, whose samples always smelled of H_2S, was 209. Sixteen genera or species occurred exclusively in the sand, but most of these represented a single occurrence. There were 6 organisms which occurred only in the sulfur patches in the aquaria, 5 which occurred exclusively in the non-sulfurous areas, and 19 which occurred exclusively in the pond samples. These 19 included 4 species of *Metopus* and 3 Ctenostomata; evidently the samples from which these were observed were anaerobic. In addition, the pond samples appear to differ in other, but poorly defined ways. Evidently a considerably larger number of samples (than 15) should be studied for definite conclusions as to spot differences in the bottom of ponds. Nevertheless, some organisms which occurred frequently in the other three locations were practically lacking there. These included *Chlamydodon memosyne*, *Coleps*, *Holosticha*, *Metacystis*, *Pleuronema*, *Uronema*, and *Protocrucia pigerrima*. It seems probable that the absence of these 7 ciliates represents an overall difference; *i.e.*, some condition in the ponds is different from those in the other situations, and that we are not here dealing with microclimatic effects. On the other hand, it seems reasonable that the differences between sand and aquaria, and between the sulfurous and non-sulfurous patches in the aquaria are probably microclimatic.

Certainly the data show differences, and show the richness and importance of the ciliate fauna. The data also illustrate the difficulties of obtaining a representative sample.

DISCUSSION

Greater emphasis should be given to the biochemical exchanges at the mud-water interface. Zicker, Berger, and Hasler (1956) reviewed briefly the matter of phosphorus release, and the literature pertaining thereto. Hays, McCarter, and Cameron (1952) noted that the active zone concerned in this diffusion of phosphorus to the water was about a millimeter in thickness. Ohle (1956), stressing the importance of completely accounting for CO_2 production in bioactivity (he prefers this term to productivity), pointed out that in deep lakes anaerobic CO_2 formation was much less than shallow lakes. He states that mineralization continues after the DO supply has been exhausted, and CO_2 accumulation gives a more accurate picture of bioactivity than does the O_2 deficit.

Assuming that all such discussions point to the importance of the mud-water interface, it follows that much more needs to be known

about the kinds and distribution of the organisms there. Most of the work has concerned larger organisms than microscopic algal and protozoan cells, and dredges or scoops taking large samples have been used. Sanders (1960) used such a device in his Buzzards Bay studies, but he also used a Phleger sampler for cores, and Wieser (1960) depended completely on cores. It appears that coring samples adequately a given situation for small organisms, and that coring methods will be improved from time to time. Patchiness of organisms probably is due to differences in bottom composition, and the remedy for this is coring over a considerable area, or ability to observe the bottom.

Actually, the worst gap in our knowledge of the marine benthic inhabitants seems to concern the protozoa, microscopic algae and certain bacteria, especially those which accumulate elemental sulfur. There are very few published accounts of the taxonomy and ecology of these groups, except for small sub-groups such as Foraminifera. Schaeffer (1926) probably has more information on marine amebas than can be found elsewhere. Kahl (1930–35) gives descriptions and figures of many marine ciliates. Faure-Fremiet (1950) also has some interesting studies on sand-dwelling ciliates, that consider certain aspects of their ecology not usually taken into account. It is difficult to separate the sand-dwelling ciliates from those at the surface of the mud, although Faure-Fremiet gives a list of sand dwellers, mostly from Kahl's work but also some new species. Webb (1956) in studies of the ecology of brackish-water ciliates found many of the forms encountered in the present work, as interface species. Manifestly, grain size and mud-sand factors which Sanders (1958) found operative for larger animals, operate for ciliates and probably other protozoa also. But most of the other benthic microorganisms are discussed in scattered papers such as those of Herdman (1921, 1922, 1923, and 1924) on benthic dinoflagellates. If we are going to arrive at valid conclusions on distribution, productivity, and ecology of the mud-water interface, the above three groups must be studied more intensively.

The papers of Wieser (1960) and Sanders (1960) aim "at as complete a picture as possible of the various vectors determining the structure and dynamics of a marine benthic community." Wieser discusses 9 groups of microscopic or almost microscopic metazoans. Sanders considers 11 groups of somewhat larger metazoa. The two papers complement each other well, presenting a good picture of the larger organisms of the Buzzards Bay area studied. Before one generalizes too much from reading these papers, it must be remembered that: a) they report on limited areas; b) the bacteria, algae, and protozoa may be presumed to have a much faster reproductive rate; c) it is not known to what extent these last three groups were present. Through the courtesy of Dr. Sanders, the writer examined Buzzards Bay and Eel Pond core samples in the summer of 1959. The top few millimeters of the Buzzards Bay samples contained largely fecal pellets and numerous protozoa, the dominant group being colorless euglenids, followed by ciliates. Samples from the Eel Pond at the same time showed numerous ciliates and euglenids. But neither locality contained nearly as many organisms as the locations shown in the Rhode Island studies. We may assume the same bottom patchiness for algae and protozoa, as for other organisms, and ascribe it to such factors as grain size, organic content, *etc.*, (Holme 1949). It is also to be expected that situations near shore, and in shallow water will contain larger and more varied populations than offshore situations. The present account bears this out, and emphasizes the necessity for quantitative as well as qualitative studies. Mare (1943) obtained rather meager results for protozoa both as to quality and quantity, but her results were mostly based on culturing of bottom samples, rather than direct examination. Only a few of the benthic organisms last very long in cores brought into the laboratory or in cultures made from such cores. Bottles suspended several feet off the bottom at the end of the Scripps Pier at La Jolla, in the summer of 1959, accumulated silt and sand in 48 hr, but the numerous

algae and protozoa they accumulated were largely plankton forms, not benthic.

In conclusion, we need a long-term study, at least two years, into the kinds and numbers of microscopic algae, sulfur accumulating bacteria and protozoa, from a considerable variety of marine mud-water interface samples. Such a study would add to the more numerous ecologic and taxonomic studies of the larger benthic organisms. Core samples appear to be an excellent device for securing such samples, which should be studied alive where possible, but also by culture methods and after preservation.

This study might well be divided among several specialists, and should include physico-chemical determinations on the bottom material.

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THE ENIGMA OF GEORGES BANK SPAWNING

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ABSTRACT

The drift of bottles and transponding drift buoys over the Georges Bank area show that, with the exception of midsummer when the Georges eddy is most pronounced and southerly winds predominate, surface drift is offshore in the direction of the slope water band. Indications are that the currents below the surface move at a slower rate than at the surface, but in a similar direction. The effects of offshore drift, time and location of spawning, vertical distribution of eggs and larvae, and length of pelagic life on the dispersal and survival of eggs, larvae, and juveniles of commercially important foodfishes are discussed. It appears from observations on haddock and herring that under average conditions most fish eggs and larvae are carried away from Georges Bank and lost to the fishery, that only under unusual hydrographic conditions are the eggs and larvae retained in the area, and that the year class strength of the various species inhabiting Georges Bank is dependent in part upon non-tidal drift.

INTRODUCTION

The Georges Bank area, because of its tremendous productivity resulting from strong tidal stirring, is a favorite habitat of many demersal and pelagic species of fish. Georges Bank not only is one of the most productive fishing grounds in the North Atlantic, but also is the principal spawning area for many species of fish and shellfish. Some of the commercially important species that spawn there are haddock (*Melanogrammus aeglefinus*), cod (*Gadus callarias*), pollock (*Pollachius virens*), whiting (*Merluccius bilinearis*), red hake (*Urophycis chuss*), cusk (*Brosme brosme*), herring (*Clupea harengus*), American dab (*Hippoglossoides platessoides*), yellowtail flounder (*Limanda ferruginea*), gray sole (*Glyptocephalus cynoglossus*), and the sea scallop (*Placopecten magellanicus*). The approximate times of maximum spawning for these species on Georges Bank are as follows: pollock, December–February; cod, January–March; gray sole, January–April; haddock, February–April; American plaice, March–May; cusk, April–May; whiting and yellowtail, May–July; red hake, June–September; and herring and sea scallop, September–October.

All these fish are bottom spawners, but the larvae of all species and the eggs of all species except herring drift passively in the upper water layers for considerable periods after spawning. In view of the non-tidal circulation pattern as deduced from drift-bottle, and transponding drift-buoy studies, and of the proximity of Georges Bank to the easterly flowing band of slope water, it is somewhat puzzling as to how these populations of fish maintain themselves in the area. It is the purpose of this paper to illustrate the effect of non-tidal drift upon the dispersal of eggs and larvae from Georges Bank using data collected during the haddock and herring spawning seasons and to discuss the consequence of physical and biological factors upon the abundance of the various species of fish inhabiting the Georges Bank area.

SOURCES OF MATERIAL

The data on haddock spawning and the distribution and drift of haddock eggs and larvae are based on collections made by the U. S. Fish and Wildlife Service during the spring months of 1953, 1955, 1956, and 1957 (*Albatross III* cruises 46, 48, 57, 58, 60, 71, 72, 73, 90, 92, 93, 94, and 95) as part of a program designed to study the early life history of haddock. The authors are particularly indebted to Messrs. Robert R. Marak and David Miller of the U. S. Fish and Wildlife Service Biological Laboratory, Woods Hole, Mass., for assistance in the collection and processing of these data. Data on the spawning location of herring are based on collections made by the U. S. Fish and Wildlife Service and the Fisheries Research Board of Canada during the fall months of 1956 and 1957 (*Silver Bay* cruises 1 and 2, and *Haren-*

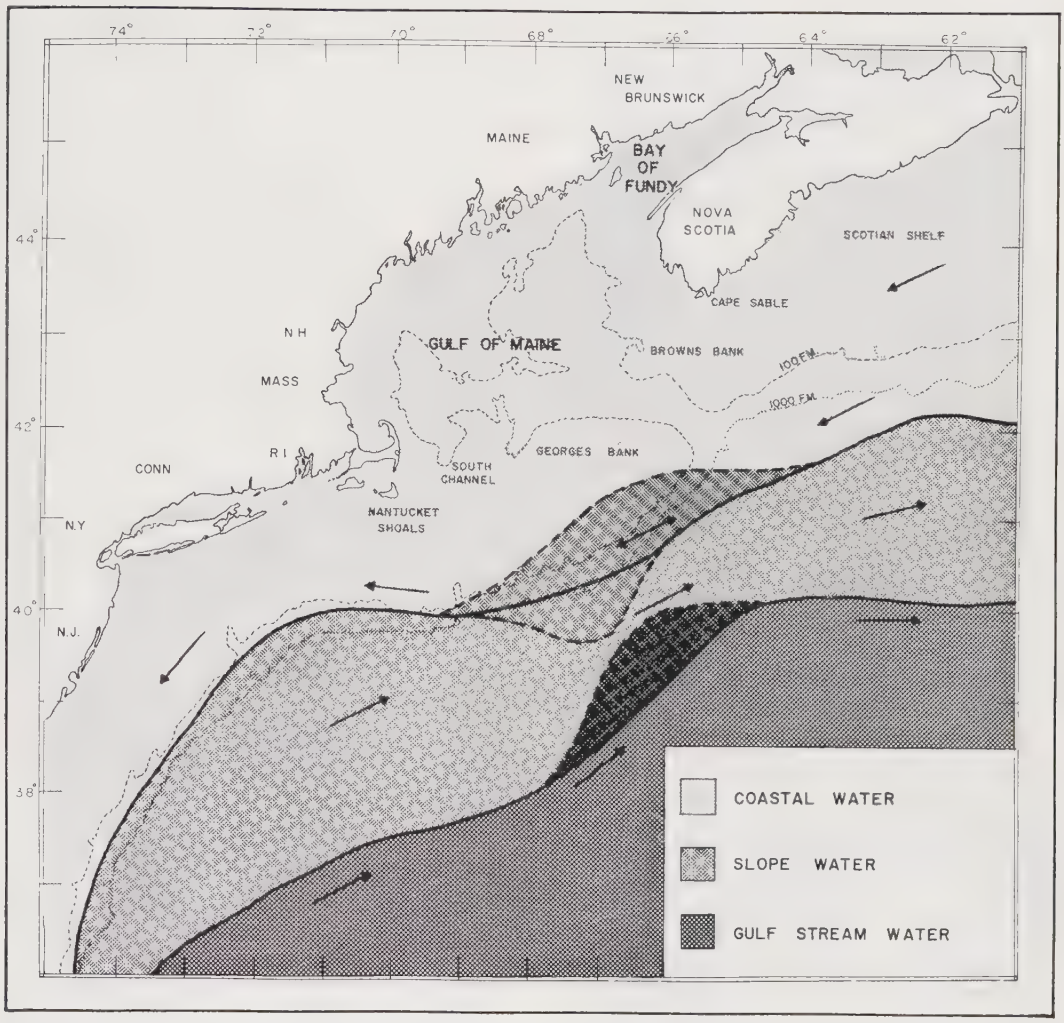

FIG. 1. Diagrammatic representation of the areal extent and movement of coastal, slope, and Gulf Stream water off the coast of Nova Scotia and New England.

gus cruises 5, 6, 17, and 18) as part of a program designed to study the early life history of herring.

Cruises during both these programs were of approximately 2 weeks' duration and the area of coverage included the Bay of Fundy, Gulf of Maine, Browns Bank, and Georges Bank. During these cruises Hardy Plankton Recorders (Hardy 1936) were towed continuously at the surface and 10 m; and 15-min surface and oblique (10 m) meter-net tows, bathythermograph lowerings, surface salinity samples, and drift bottle releases were made at specified stations. The drift bottles were of 8-fluid-ounce capacity. Twelve bottles were released at each station, 6 with sand ballast and 6 without. Drift-bottle data were processed under contract with the Woods Hole Oceanographic Institution under the direction of Mr. Dean F. Bumpus.

GENERAL HYDROGRAPHY OF COASTAL AND OFFSHORE WATERS OF NEW ENGLAND AND NOVA SCOTIA

In sequence from the coast of New England and Nova Scotia there are three distinct bands of water having well-defined temperature and salinity characteristics. They are

the relatively cool and less saline (<35‰) *coastal water* covering the continental shelf and often extending near the surface well beyond the 100-fathom contour; the *slope water* having intermediate values of temperature and salinity (35–36‰); and the *Gulf Stream* water of relatively high temperature and salinity (>36‰) (Iselin 1936). The transition from one zone to the next is rapid, with considerable variations in temperature and salinity taking place within a very few miles. The general topography of the area under discussion and a diagrammatic representation of these three oceanographic regions are given in Figure 1.

The slope water, which lies between the coastal water having a southwesterly drift and the Gulf Stream moving swiftly towards the northeast, is a mixing zone for coastal water which has escaped over the continental shelf and Gulf Stream water which has been carried north of the current's path (Iselin 1936). A regular feature of the slope water is an easterly flowing current, the energy for which comes from a frictional drag when momentum is transferred across the northern edge of the Gulf Stream (McLellan 1957). This slope water band extends southwest only as far as Cape Hatteras.

There are marked flucuations in the relative position and areal extent of the three water masses in time and space (Fig. 1). Slope water has frequently been observed to overflow onto Georges Bank; coastal and Gulf Stream water meet at times off the southern edge of Georges Bank; cold patches of coastal water sometimes occur along the northern edge of the Gulf Stream; and eddies of warm Gulf Stream water are from time to time thrown off into the slope water (McLellan 1957).

The discharge of land drainage into the coastal water maintains a lower salinity and density in the surface layer there than in the surface layer offshore. The hydrostatic forces tend to drive this surface layer offshore and this, coupled with the Coriolis acceleration, results in a southwesterly flow along the shelf (McLellan 1957). Tidal currents, bottom topography, river runoff, and winds tend to disrupt the general southwesterly drift of coastal water along the continental shelf, and the circulation pattern in an area such as the Gulf of Maine is quite complex. The dominant non-tidal circulation of the Gulf of Maine as described by Bigelow (1927) and shown schematically in Figure 2 comprises a general counterclockwise eddy around the basin of the Gulf with an indraft on the southern side of the Bay of Fundy along the Nova Scotian shore, a separation of the outflow of the Gulf to the south, and an easterly drift along the northern side of Georges Bank, the latter being the center of a clockwise eddy. The average rate of surface drift is in the order of 3–4 miles per day. Recent drift-bottle studies (Day 1958, Bumpus 1958 and 1960) reveal that Bigelow's July–August pattern showing a relatively closed circulation seems to evolve with the seasons as a result of vernal warming and the consequent formation of density structure. These studies show that during February and March the Gulf eddy is ill-defined and there is a strong movement of water southward out of the South Channel. By late April the two counterrotating eddies begin to build up with the appearance of a northeasterly drift along the northern edge

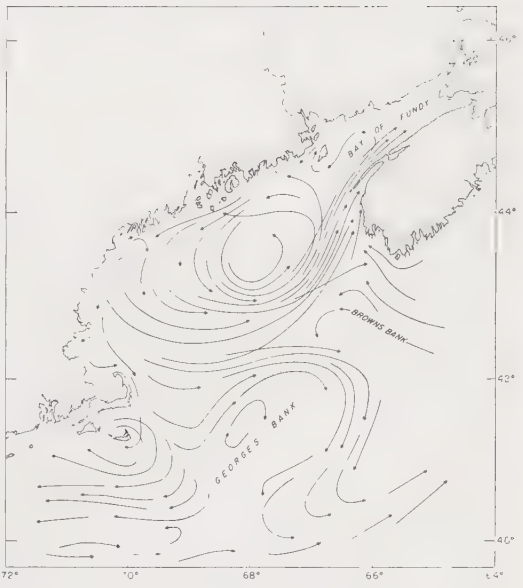

FIG. 2. Schematic representation of the dominant non-tidal circulation of the Gulf of Maine, July to August. (After Bigelow.)

of Georges Bank where the two eddies become confluent. The dual-eddy system continues throughout the summer, but by early fall the Georges eddy and the southern side of the Gulf eddy begin to weaken and the indraft into the Bay of Fundy is limited to north of 43° N. In winter the western side of the Gulf eddy weakens and the Georges eddy gives way to an easterly offshore drift. At this time the density of the waters over the continental shelf becomes more like that of the corresponding layer beyond the 100-fathom curve, coastal currents die away, and the predominantly northwest winds force large masses of water offshore. There is no evidence from drift-bottle work of any movement across Georges Bank from south to north, although surface water occasionally drifts northward from the continental shelf to the west of Nantucket Shoals during the late summer.

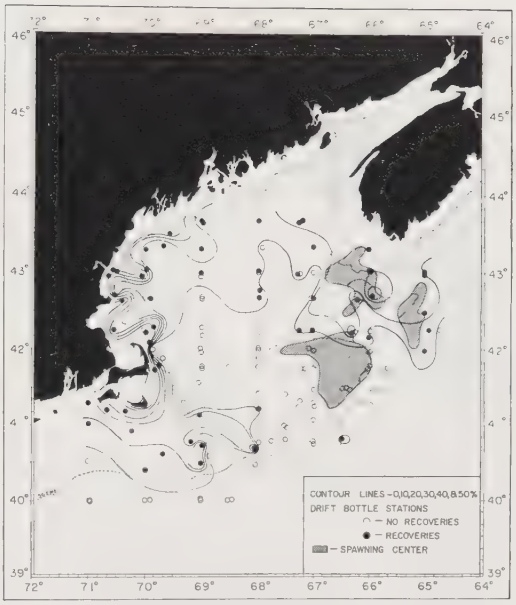

FIG. 3. Haddock spawning locations, drift-bottle release stations, and percentage drift-bottle recovery between Cape Sable, N. S., and Normandy Beach, N. J., *Albatross III* cruises 46 and 48, March 19–April 2 and April 24–May 8, 1953.

HADDOCK-SPAWNING AREAS AND THE DRIFT OF BOTTLES AND TRANSPONDING DRIFT BUOYS

The spawning areas of haddock were determined from the distribution of early-stage eggs caught in meter-net and Hardy Plankton Recorder tows. The period of embryonic development included is from fertilization to the approach of the germinal ring to an equatorial position. At the prevailing water temperatures on Georges Bank during the spawning period (40° to 44°F) this grouping includes eggs up to 8 days old. The locations of appreciable haddock spawning and of drift-bottle releases and the percentage recovery of drift bottles along the shoreline between Cape Sable, Nova Scotia (43°30′ N, 65°30′ W) and Normandy Beach, New Jersey (40°00′ N, 74°04′ W) are shown in Figures 3, 4, and 5. Only drift-bottle returns within this area have been considered in determining percentage recovery, as there is no evidence that larval fish carried beyond this area return to the Gulf of Maine as juvenile or adult fish.

In all years the distribution of early-stage eggs revealed that Georges Bank and Browns Bank were the principal spawning areas for haddock. Limited spawning oc-

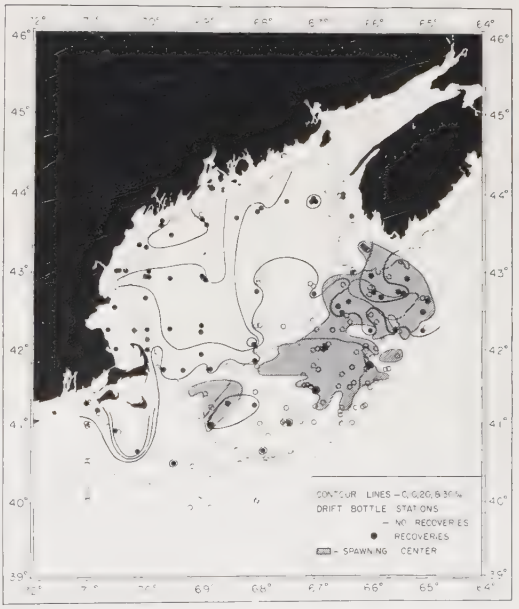

FIG. 4. Haddock spawning locations, drift-bottle release stations, and percentage drift-bottle recovery between Cape Sable, N. S., and Normandy Beach, N. J., *Albatross III* cruises 57, 58, and 60, February 21–March 2, March 19–April 1, and April 19–May 3, 1955.

FIG. 5. Haddock spawning locations, drift-bottle release stations, and percentage drift-bottle recovery between Cape Sable, N. S., and Normandy Beach, N. J., *Albatross III* cruises 71, 72, and 73, February 20–March 2, March 21–31, and April 17–28, 1956.

curred in the South Channel and along the New England coast. These spawning locations coincide with those depicted by Walford (1938). With the exception of 1955 the total production as indicated by the average number of eggs/m^3 in the upper 10 m of water was greater on Georges Bank than on Browns Bank. In all years Georges Bank spawning occurred in an area of minimum drift-bottle returns. Drift bottles released on Georges Bank tended to drift southwesterly and out of the area. The majority of the meager recoveries from the areas of spawning were from the coastline between New Jersey and Cape Hatteras and from foreign shores. Most of the locations in which spawning occurred in the Browns Bank area coincided with areas from which there was a relatively high percentage of drift-bottle recoveries. Bottles released on Browns Bank and off southwestern Nova Scotia tended to drift northwesterly and beach along the shores of western Nova Scotia, New Brunswick, and New England as far south as Cape Cod (Day 1958). Surface drift during the haddock-spawning season as indicated by drift-bottle data is offshore over Georges Bank and inshore over Browns Bank. Plots of the relative distribution of eggs and of larvae, assumed to have hatched from these eggs, showed a similar southwesterly drift over Georges Bank and a northwesterly drift from Browns Bank.

Although it has been possible in each year to demonstrate a southerly movement of haddock eggs and larvae from the Georges Bank spawning center, neither eggs nor larvae were ever found off the southern edge of the Bank in the slope water band. Drift-bottle data indicate such a drift, but furnish no information as to the actual trajectory of the bottle between the place of launching and recovery. In order to obtain more detailed information on the movement of surface water over Georges Bank, transponding drift buoys were set out in a concentration of haddock eggs and their drift observed during April, May, and June, 1957. The details of the transponding drift buoys used in this work have been described by Bumpus, *et al.* (1957). The buoys were 20 ft long, 6 in. in diameter, and ballasted to float vertically with 2 ft of freeboard surmounted with a 13-ft whip antenna. When the buoy's receiver was energized by a tone-modulated signal from the *Albatross III*, the buoy's transmitter responded with signals which in turn were homed on by the vessel's radio direction finder. Repetition of this procedure and suitable maneuvering of the vessel brought the buoy within visual range.

Concentrations of early-stage haddock eggs were located by means of meter-net and Hardy Plankton Recorder tows, and transponding drift buoys were released in the area of maximum spawning. The transponding drift buoys used in this study were named *Mike*, *India*, *November*, and *Hotel*. The location of haddock spawning and of drift-bottle releases between April 2 and May 16 and of transponding drift-buoy releases between April 15 and May 23, the percentage drift-bottle recovery between Cape Sable, N. S., and Normandy Beach, N. J., and the drift of transponding drift buoys are shown in Figure 6.

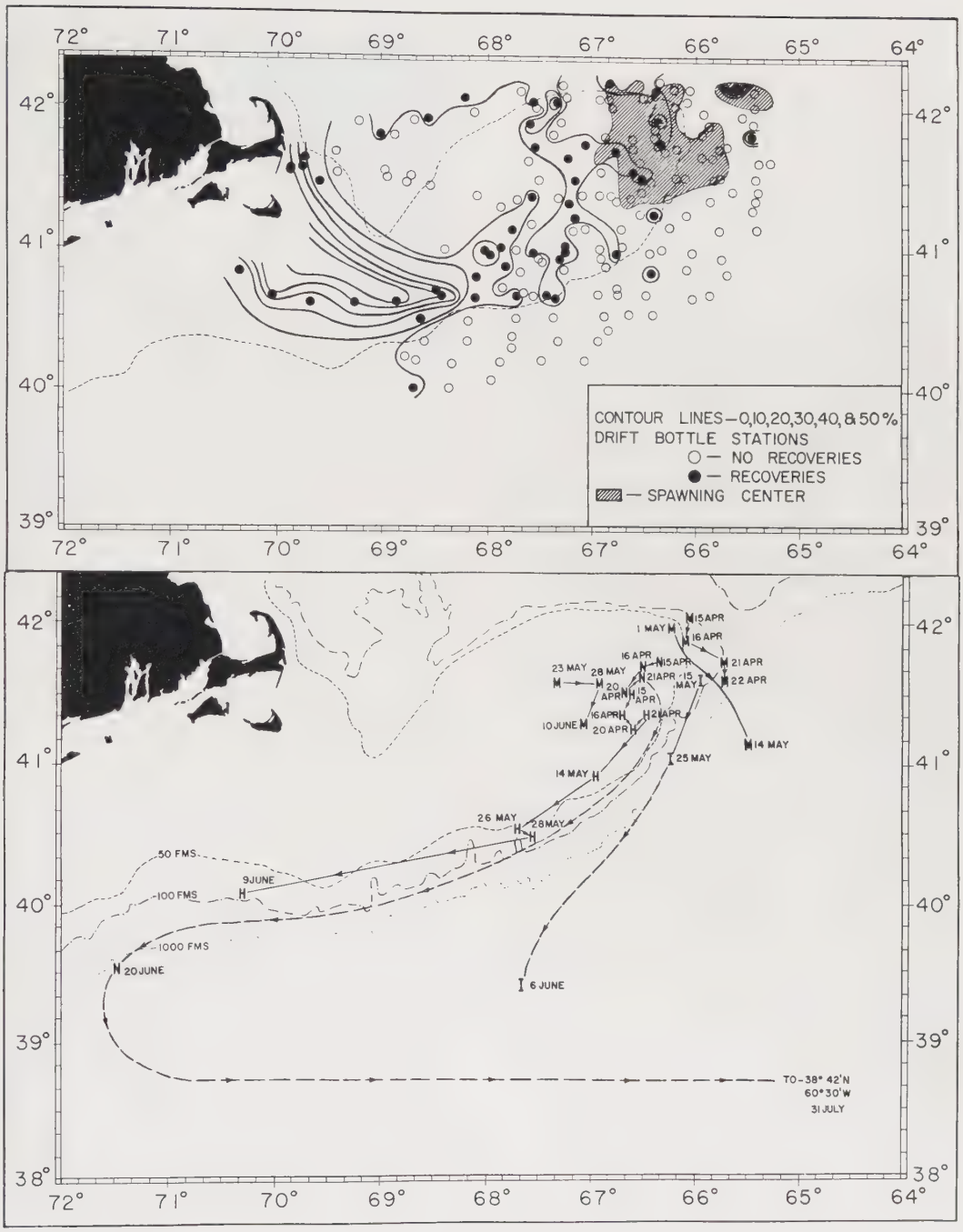

FIG. 6. Haddock spawning locations, drift-bottle and transponding drift-buoy release stations, percentage drift-bottle recovery between Cape Sable, N. S., and Normandy Beach, N. J., and transponding buoy drift, *Albatross III* cruises 90, 92, 93, 94, and 95, April 12–17, April 25–May 2, May 8–16, May 22–29, and June 5–12, 1957.

Buoys set out at the northeast part of Georges Bank (*Mike* and *India*) moved southerly into deep water at velocities greater than 5 miles/day. Buoy *Hotel* moved slowly (approximately 1.5 miles/day) in a southwesterly direction until May 28 and then drifted rapidly (approximately 10 miles/day) in a west southwesterly direction. Buoy *November*, which failed to respond after April 21, was sighted on June 20 just east of the Hudson Canyon, after having probably moved along a similar course as *Hotel*. Buoy *November* was subsequently sighted in the Gulf Stream on July 31, 500 miles to the eastward of its June 20 position. The drift of the transponding drift buoys substantiates the previously noted clockwise circulation around Georges Bank (Fig. 2) but what is more important it also conclusively demonstrates a southerly movement of surface water away from the area of spawning on Georges Bank and out into the slope water band.

In contrast to previous years, considerable numbers of bottles released on Georges Bank in 1957 were recovered. Most of these bottles beached along the southern shore of Cape Cod and on Nantucket and Martha's Vineyard. However, a few bottles set out in the area of transponding drift-buoy release stations on the northeast part of Georges Bank moved in a northerly direction and were recovered along the coasts of Nova Scotia and New Brunswick. This suggests a differential drift between surface and depth and that the drift bottles, which float in the upper few feet of water compared to the 18-ft draft of the transponding drift buoys, were more subject to the predominantly southwesterly wind conditions existing at this time. It appears that bottle drift is not always a reliable indication of the dominant non-tidal circulation.

The movement of the transponding drift buoys and bottles indicates that at this time of the year the non-tidal circulation over Georges Bank is such that eggs and larvae in the surface layers would be carried out into the slope water zone or into the coastal waters west of Cape Cod.

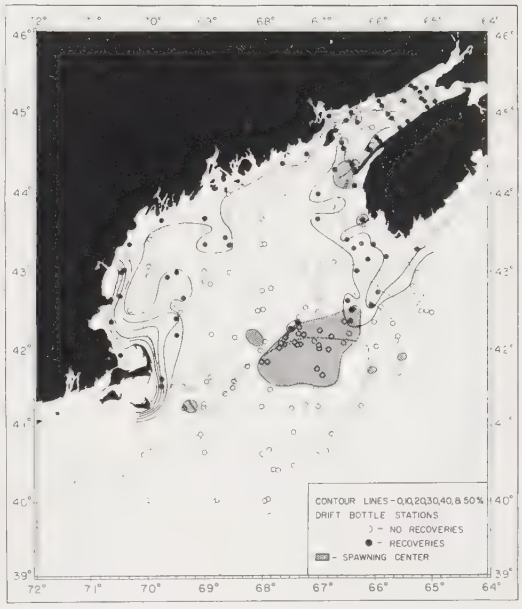

FIG. 7. Herring spawning locations, drift-bottle release stations, and percentage drift-bottle recovery between Cape Sable, N. S., and Normandy Beach, N. J., *Silver Bay* cruises 1 and 2, September 21–October 5, and October 15–25, 1956, *Harengus* cruises AH5, AH6, 17, and 18, September 19–October 4 and October 16–November 8, 1956, September 9–26 and October 7–25, 1957, and *Albatross III* cruise 104, October 9–17, 1957.

HERRING-SPAWNING AREAS AND THE DRIFT OF BOTTLES AND TRANSPONDING DRIFT BUOYS

The location of spawning areas of herring is based on the distribution of 5- to 7-mm larvae as determined from meter-net and Hardy Plankton Recorder tows during September and October, 1956 and 1957. This length range approximates the range in hatching size of larval herring and in the absence of egg samples from the bottom affords the best available approximation of spawning location. The location of appreciable spawning and of drift-bottle releases, and the percentage recovery of drift bottles Beach, N. J., are shown in Figure 7.
between Cape Sable, N. S., and Normandy

The main area of spawning indicated by the distribution of newly hatched larvae was along the northern edge of Georges Bank. Limited spawning occurred off the west coast of Nova Scotia and in the South Channel. Herring may also have spawned to some

extent in shoal water areas along the coast of Nova Scotia, New Brunswick, and Maine not covered in these surveys. However, the magnitude of production, as indicated by the number of larvae/m^3 in the upper 10 m of water, was so much greater over Georges Bank than in other areas that it is evident this is the principal fall spawning area in the Gulf of Maine.[1] Spawning also occurs in the Fundy region during the spring, but it is very light and very much less in importance than the heavy autumn spawning (Tibbo, *et al.* 1958).

As with haddock, herring spawned on Georges Bank in an area of minimum drift-bottle returns. The areal extent of the stations from which there were no drift-bottle recoveries was considerably greater than it was during the spring months. It was only from stations along the coast and over Browns Bank that recoveries were made. Transponding drift buoys released over the western part of Georges Bank during October and December, 1957, moved in an easterly direction at speeds of approximately 7 miles/day (Bumpus 1958). The dominant easterly offshore drift of buoys and the almost complete void of local drift-bottle returns from the Gulf of Maine and Georges Bank show that during the autumn and winter the dual-eddy system breaks down and the Georges eddy gives way to an easterly offshore drift.

The non-tidal circulation over Georges Bank during herring spawning differed markedly from that during haddock spawning. In the spring the net surface movement across Georges Bank was southerly and southwesterly, while in the fall the net surface movement was easterly. Herring larvae in the surface layers over Georges Bank would have been carried more rapidly out into deep water than haddock eggs and larvae. It appears that herring larvae had less chance of being retained in the area or of being carried into the Gulf of Maine and the Bay of Fundy than did haddock larvae.

[1] It is of interest to note that only during the fall spawning season do otter trawlers capture appreciable numbers of herring over Georges Bank; little is known about the distribution of these Georges Bank fish at other seasons of the year.

DISCUSSION

Data on the drift of bottles and on the movement of transponding drift buoys show that, with the exception of midsummer when the Georges eddy is most pronounced and southerly winds predominate, surface drift over the Georges Bank area is offshore in the direction of the slope water band. It appears, therefore, that at most seasons of the year fish eggs and larvae in the surface layers would be carried away from Georges Bank and lost to the fishery. However, before we can conclude that this is the fate of the majority of eggs and larvae produced on Georges Bank, we must consider the differential rate and direction of drift between surface and depth, the vertical distribution of eggs and larvae, the effect of the warm slope water on survival, the length of pelagic life, and the ability of larval and juvenile fish to move independently of the existing currents.

Surprisingly little is known about the subsurface currents in the Georges Bank–Gulf of Maine area. Most of the information available is based on inferences from temperature and salinity observations (Bigelow 1927), and the only extensive direct current measurements made in the area have been surface observations. Strong tidal mixing over most of the area keeps the water mixed from top to bottom, so that little vertical stability develops even in the warmest months. Strong temperature and density gradients are usually found only along the edge of the continental shelf and in isolated bays along the coast. The distribution of temperature and salinity suggests that in general the circulation pattern deduced from surface observations is effective to at least 100 m although the velocities are somewhat lower in the deeper water than at the surface. With increasing depth, however, the direction of flow is more and more influenced by the contour of the bottom. Wind currents which may accentuate or weaken the prevailing drift or at times cause the surface water to move in a different direc-

tion than subsurface water are confined to the upper 10 to 20 m of the water column.

Ballasted drift bottles which sank and were picked up on the bottom or at mid-depths by fishermen showed a uniform southwesterly movement along the southern part of Georges Bank and a general southerly movement out of the South Channel (Day 1958). The rate of drift of these bottles was considerably less than that of bottles which remained at the surface. Experiments in which buoys have been rigged with parachute drogues of varying lengths also showed that in general the direction of flow was similar at depth, but that the rate of drift decreased with an increase in the depth of the drogue (Bumpus 1958).

Along the southern edge of Georges Bank, in the deeper parts of the Gulf of Maine Basin, and in the Eastern Channel, which separates Georges and Browns banks, the direction of water movement sometimes differs from that in the surface layers. From late summer through early spring, slope water enters the Gulf of Maine in varying pulses along the bottom of the eastern side of the Eastern Channel. The outward flow of slope water is usually along the western side of the Eastern Channel (Bigelow 1927). The general tendency of movement along the bottom within the basin is northward along the Nova Scotian slope and veering through west to southwest across the basin towards the offing of Massachusetts Bay. It is only along the bottom of Eastern Channel and the southern edge of Georges Bank that eggs and larvae could drift in an opposite direction from those in the surface and intermediate layers.

Vertical distribution studies of larval and juvenile haddock made in the Georges Bank area in 1958 (*Albatross III* cruise 111) using specially designed high-speed samplers towed in series at depths of 0, 10, 20, 30, 40, 50, and 75 m showed that in all locations, depths, and times the maximum abundance of larval and juvenile haddock (5–30 mm) was in the upper 20 m of water. Very few haddock were caught at depths greater than 20 m and the larger postlarvae and juveniles tended to be concentrated in shoaler depths than the smaller larvae. Although haddock eggs are known to occur in the deeper water layers (Walford 1938), indications are that the abundance of haddock eggs also decreases with depth, for in all cruises made in 1953, 1955, 1956, and 1957 the vast majority of eggs were collected in the plankton recorder towed at the surface.

Conjectures concerning the vertical distribution of larval herring in the Georges Bank area are based on generalizations inferred from their distribution and abundance in the upper 10 m of water. During the surveys of 1956 and 1957 more larval herring were caught at 10 m than at the surface during both the day and night. The number and average length of herring larvae, but not of other species, were greater at the surface and 10 m during the night. Indications are that the depth of maximum abundance of larval herring is below 10 m, that larval herring move up towards the surface layers during the night, and that the extent of these diurnal migrations increases with an increase in the size of the larvae.

Little is known of the vertical distribution of the eggs and larvae of other species found in the area, but indications from these surveys are that the eggs of most species are concentrated in the upper 10 m of water, that gadoid larvae are more abundant in the surface layers (0–20 m) and that flatfish larvae tend to be more abundant below 20 m. Herring is the only species in which there were indications of diurnal vertical movements.

The presence of the slope water band off the southern edge of Georges Bank affects the survival of larval fish in two ways. Firstly, any larval fish drifting into this zone would be carried in a northeasterly direction away from Georges Bank and the continental shelf. Secondly, because of the marked differences in the temperature of coastal and slope water, it is possible that larval fish transported from one zone to the other would be subject to a temperature change beyond the range of their thermal tolerance. That temperatures in the slope water band are at times lethal to species of larval fish endemic to the Gulf of Maine–Georges Bank area is evidenced by observations of the mortality

of yellowtail flounder and whiting (Colton 1959).

Estimates by Bigelow and Schroeder (1953) indicate that 3 months would be an average time for the duration of pelagic life for the species of fish mentioned in this paper. However, there is a variation in the length of pelagic life with species and possibly within species according to location and environmental conditions. More recent observations indicate that the young of some species of fish remain in the surface layers for considerably longer periods than previously expected. During the plankton recorder surveys of the Georges Bank area in 1953, 1955, 1956, and 1957, juvenile herring (40–60 mm) were frequently found in the surface layers in February, March, and April; and juvenile pollock, cod, and red hake were found as late as May and June. It was also observed that there was closer association of haddock and whiting with the common red jellyfish (*Cyanea*) as the fish grew larger. Haddock and whiting longer than 20 mm were never found in areas where *Cyanea* was not present. Other species including hake and cusk were also frequently found living under the bells of *Cyanea* and this association, which has been observed previously in both American and European waters (Damas 1909, Russell 1928, Bigelow and Schroeder 1953), has the effect of limiting their depth distribution to the surface layers and of extending the period in which these fish can be considered true members of the planktonic community and subject to involuntary drift.

Horizontal tows at 10-m depth intervals made in the Gulf of Maine during August and September, 1957 (*Albatross III* cruises 99 and 102), with an Isaacs-Kidd midwater trawl (Isaacs and Kidd 1953) modified to operate as an opening-closing net showed that juvenile haddock were still concentrated in the surface layers 5 or 6 months after the time of maximum spawning. The average size of these juvenile haddock was 105 mm and an analysis of their depth distribution in the upper 100 m revealed that over 90% of the fish occurred between 10 and 30 m, that the depth of maximum abundance was at 20 m during the day and night, and that over 90% of the positive tows were made in areas where *Cyanea* was present.

Bottom tows with an otter trawl in the same areas showed that there was a small overlap between the size of the fish on the bottom and those at middepth. The average size of juvenile haddock on the bottom was 125 mm. Indications are that juvenile haddock live in association with *Cyanea* throughout their pelagic life and begin to take to the bottom at a length of about 100 mm.

The ability of larval and juvenile fish to move independently increases with size and by the time the metamorphic period is completed and the young fish have assumed adult characteristics (juvenile stage) they are capable of undertaking fairly extensive migrations. The duration of the larval period varies with species, being considerably longer in the herring, for example, than in haddock. The approximate size at which the various species complete metamorphosis is as follows: herring—40 mm, gadoids—20 mm, American dab—30 mm, gray sole—45 mm, and yellowtail flounder—15 mm. Postlarvae of species such as herring, in which metamorphosis extends over a considerable period, are capable of greater independent movement than are the postlarvae of species that have a short larval life. With the exception of the flounders and herring, this ability for independent movement is nullified to a great extent by the fact that these movements are confined for the most part to areas in which *Cyanea* occurs. Even though the young fish can and do move independently, their net movement is controlled in part by the drift of *Cyanea* and thus their distribution is still dependent to some degree upon the non-tidal circulation. It appears then that the dispersal of the majority of species from the spawning areas on Georges Bank is controlled primarily by non-tidal drift, that this involuntary movement is in effect for a 4- or 5-month period, and that not until the juvenile fish reach the bottom do they begin to control their distribution. Such an extensive pelagic period is in agreement with the average drift rate of bottles and the distribu-

tion of young-of-the-year haddock on the bottom during the fall of the year.

Young-of-the-year haddock are rarely found on Georges Bank in the fall. The area of maximum abundance in most years in which bottom surveys were made was in deep water (over 90 fathoms) in the South Channel and the southwestern part of the Gulf of Maine. Young-of-the-year haddock were also found in other parts of the Gulf and on Browns Bank. Only in 1948 and 1950 were young-of-the-year haddock found west of Georges Bank when large concentrations occurred in shoal water (20–50 fathoms) off southern New England and Long Island (Colton 1955). The 1948 and 1950 year classes are two of the strongest broods of Georges Bank haddock which have occurred since the collection of such statistics was begun in 1928 (Chase 1955). The young fish found off southern New England and Long Island most likely migrated back to Georges Bank by the following spring, as few one-year or older haddock are ever caught west of Nantucket Shoals. It is postulated that in most years the abundance of Georges Bank haddock is dependent upon spawning taking place in other areas (principally Browns Bank) and that strong year classes occur in those years when the eggs and larvae are retained on Georges Bank or in the coastal waters off southern New England and Long Island. It is possible that some young haddock take to the bottom further south, but there is no evidence that this happens.

The herring fishery in the Gulf of Maine is principally a sardine fishery. One- and 2-year-old fish make up the bulk of the catch and the fishery is centered along the coast of Maine and New Brunswick. Considering the location of the fishery and the dominant non-tidal drift on Georges Bank during the herring-spawning season, it is doubtful that herring spawned on Georges Bank contribute to this fishery. It is possible that in some years strong easterly or southerly winds would alter the dominant circulation pattern, but in general, hydrographic conditions over Georges Bank during the fall of the year are even less favorable for the retention of larvae over Georges Bank or for a northerly drift into the Gulf of Maine than during the spring. Herring larvae that drift westerly from the Georges Bank area might migrate back up along the coast, but there is no evidence to support this. Population studies based on parasitological and serological methods (Sindermann 1959) support the above conclusions. Sindermann's studies suggest that the adult herring populations spawning on the Nova Scotian coast and on Georges Bank are distinguishable, that there is only limited intermixing between the two areas, and that the sardine-size herring populating the northwestern shore of the Gulf of Maine are more similar to Nova Scotian adults than to Georges Bank adults.

It is even more puzzling as to how some of the other species which inhabit Georges Bank maintain themselves in the area. Whiting and yellowtail flounder, for example, spawn principally along the southern edge of Georges Bank and it would seem that the eggs and larvae of these species would be even more susceptible to an offshore drift. The restricted movements of the sea scallop preclude any migration, its larvae are even less capable of independent movement than larval fish, and yet the abundance of sea scallops on Georges Bank is not subject to marked fluctuations and millions of pounds are landed year after year.

Until more detailed information is obtained, no more than generalizations can be made concerning the fate of eggs and larvae produced on Georges Bank. For example, Walford (1938) concluded, on the basis of the relative numbers and distribution of postlarval haddock on Georges Bank in the spring of 1931 and 1932, that the 1931 year class exceeded in abundance that of 1932. Subsequent landings of the commercial fleet however showed that neither year class was exceptionally strong and that the 1932 year class was slightly more abundant. Nevertheless, on the basis of existing data, it appears that under average conditions most fish eggs and larvae are carried away from Georges Bank in the direction of the slope water zone and it is only under exceptional hydrographic conditions that appreciable numbers

of eggs and larvae are retained on the Bank or in nearby coastal areas. It is our feeling that egg production in the various species is always sufficient to produce a strong year class but, in general, mortalities of eggs and larvae due to drift and other factors are such that only a small percentage survive. Future work should be directed to obtain detailed information on wind conditions over Georges Bank (which appear to be a most important variable), the effect of wind on non-tidal drift, the differential rate of drift between surface and depth, the interchange of coastal and slope water along the southern edge of Georges Bank, the vertical distribution of eggs and larvae and its variation among species, the variation in the location and time of spawning and its relation to the dispersal of eggs and larvae, and the degree of association with *Cyanea* in the various species and its effect upon vertical distribution, length of pelagic life, and dispersal from the spawning areas.

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A STUDY OF WINTER FLOUNDER MOVEMENTS[1]

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ABSTRACT

Some aspects of the movements of the winter flounder *Pseudopleuronectes americanus* (Walbaum) were studied by means of tag-recovery data. No gear selectivity by sex was demonstrated for recaptured fish nor was any association found between the size of the individual and distance of recapture from the release site. An analysis of the movements of tagged individuals away from the breeding area indicates some movement to the east of the release point but this may be due to unequal fishing effort. An attempt is made to explain the return of winter flounder to the coast by means of random search postulating the presence of a reflecting barrier.

INTRODUCTION

The migration patterns and movements of fishes have been the subject of numerous investigations, and these have led to several suggestions regarding guiding mechanisms. Studies of fish homing by Hasler (1956), Hasler and Larsen (1955), and Hasler, Horrall, Wisby and Braemer (1958) indicate that the phenomenon is closely associated with orientation to various physical, chemical, and biological stimuli in the environment. Although the concepts of diffusion and oriented dispersion have been developed by Beverton and Holt (1957) as theoretical bases for dispersion and migration, few attempts have been made to apply these to field results. It is the purpose of this paper to analyze some observations pertaining to the movements of winter flounder *Pseudopleuronectes americanus* (Walbaum) away from as well as to the vicinity of a breeding area located on the coast of Rhode Island.

METHODS

Tagging experiments were conducted in Green Hill Pond, Charlestown, Rhode Island, during the winters of 1956–7 and 1957–8. Green Hill Pond is a shallow brackish water pond of approximately 475 acres surface area connected to Rhode Island Sound by an intervening pond and a narrow inlet. This pond has been observed to be a breeding area for winter flounder. A summary of the tagging data is shown in Table 1. Incomplete data on some recaptures prevented use of every tag return for this study. Tags were of the Peterson disc type attached by non-corrosive alloy pins through the nape region of the fish. Tag returns were processed by the U. S. Fish and Wildlife Service. Only lively, uninjured fish over 220 mm in total length were tagged as soon after capture as possible. The gear for capture included fyke nets fished in the pond and a small experimental otter trawl towed from an outboard motor boat. During the last two sampling intervals only the otter trawl was used. It is evident that lower returns were obtained when the fyke net was included for capturing fish, but these lower returns do not affect use of the data for the purposes at hand.

BACKGROUND AND ASSUMPTIONS

A full discussion of the mathematical basis of random diffusion and its application to animal dispersion has been given by Skellam (1951). The method of analysis applied to dispersion is similar to that used by Jones (1959) where it is assumed that movement could be divided into a directional component and an undirected or random component leading to dispersion. In this study all tagged fish were liberated close to a coastline (in the inlet of Green Hill Pond) running in an east-west direction. It is assumed that a directional component of movement, if present, would act in the direction of the coastline.

[1] Support for this investigation was obtained from the U. S. Fish and Wildlife Service, Bureau of Commercial Fisheries, Woods Hole, Massachusetts, in the form of tags and tag processing, which included payments of rewards.

TABLE 1. *Summary of Green Hill Pond winter flounder tagging data*

Date	Number tagged	Recaptured to April, 1960	% recovery
Nov/Dec, 1956	254	65	26
Feb/Apr, 1957	205	47	23
Nov/Dec, 1957	288	118	41
Feb/Apr, 1958	205	79	39
Totals	952	309	

If the distribution of catch and fishing effort is uniform in all recapture areas a straightforward interpretation of the parameters describing all movements is possible. Column 2 of the upper part of Table 2 shows that the weights of winter flounder caught are not uniform by code areas. The total effort (Column 3) is also variable, but it appears to be associated with the catch. It is recognized, therefore, that the high catch and correspondingly higher effort in code area 121, located slightly to the east of the release point, could affect the easterly component of directional movement. This must be considered in the interpretation of results.

Some aspects of the life history of the winter flounder are reviewed in light of their importance in the analysis of the tag-return data. Observations by Lobell (1939) as well as those made during this study indicate that adult winter flounder are found in cooler offshore waters during the summer months and in shallow inshore areas during winter and early spring. No adult winter flounder could be found at the original capture site during the summer months. Because of this, the analysis of tag returns is divided into two periods of 5 and 7 months. These are from June to November, during which the fish could be expected in offshore areas; and from November to June, a period which overlaps the breeding season as observed in Green Hill Pond (December–March) as well as the breeding season described by Bigelow and Schroeder (1953) which extends from January to May in New England waters. During this latter period winter flounder are expected to be found in the shallow areas containing the breeding grounds.

Wilkinson (1952) defines the reassembly of birds dispersed over a wide stretch of territory to a breeding station as diasporic migration. It has been conjectured by Beverton and Holt (1957) that most examples of fish migration are of this type, and they postulate that current direction is a guiding factor for the oriented migration of marine demersal fishes.

TABLE 2. *1958 winter flounder summary catch statistics and tag recovery data by area with a χ^2 test for similar proportions of tag recaptures in the catch*

Code area	Catch (lb)	Effort (hr)	Tag recaptures
122	155,203	1,207	13
121	360,209	4,909	29
113	35,404	463	4
112	32,162	1,492	4
131–133	49,898	2,288	7
115–117	26,758	1,589	4
Totals	659,634	11,953	61

Code area	Tag recaptures (expected)	Tag recaptures (observed)
122	14	13
121	33	29
113	3	4
112	3	4
131–133	5	7
115, 117	2.5	4

$\chi^2 = 7.447$, d.f. $= 5$, $P \sim .20$.

In this study an attempt is made to explain the return of winter flounder to the coast on the basis of the model for diasporic migration without including a guiding factor. Explicitly, a case is considered where the fish are dispersed uniformly over a strip of ocean of width w bounded on one side by a straight coast running east and west which constitutes recognizable territory and on the other by a reflecting barrier consisting of a 20-fathom depth contour located at its outer edge. The above requirements are thought to be satisfactory for the following reasons:

1. No tag returns of Green Hill fish have been reported to date outside the 20-fathom contour despite an active bottom fishery pursued immediately outside of it.
2. The model assumes that the fish are retained in the vicinity of the coast. Marked success of a local fishery with fyke nets set close to shore shortly before and after the breeding season

TABLE 3. *The proportions of male and female flounder observed and expected on the basis of equal returns from the proportions at tagging*

	Tagged fish		
	Male	Female	Total
Observed	55	153	208
Expected	62.6	145.4	208
χ^2	0.923	.397	1.320

lends support to the above assumption. Results of experimental trawling during this period also support this assumption.

Experimental trawling by the author during the 1958–9 breeding season in Narragansett Bay, Rhode Island, and Massachusetts, indicated that adult winter flounder were consistently more abundant along the margins of the bay than in the middle.

Since the model applies only to finding the coast, further searching is then generally required to establish the location of a specific breeding area. Recognition of a pond inlet is presumed to be due to olfactory perception as demonstrated by Hasler (1954) for homing salmon. However, no empirical evidence is yet available. Assuming that random search continues after the coast is reached and that it is restricted to a narrow belt in the immediate vicinity of the coast, the probability of locating an inlet per unit time would be higher than that required to locate the coast initially. Recovery of one Green Hill tagged winter flounder in each of two nearby salt ponds suggests that the same breeding area is not always successfully located during the succeeding season.

RESULTS

During the course of tagging operations, the sex of 601 tagged winter flounder was reliably recorded. These fish were 30% males and 70% females. Table 3 shows that there is no selectivity by sex at recapture. The high proportion of females does not appear to be due to differential vulnerability nor do these data suggest differences in dispersal pattern by sex for the winter flounder.

Using all the June-to-November data, a simple test for association between the size of the individual fish at tagging and the distance at recapture from the release site does not show any correlation (r=.02, n=110). Even when the partial correlation between size and distance from release site eliminating time at large is calculated, a non-significant ($r_{12.3}$=.056) association exists. According to Warfel and Merriman (1944) immature winter flounder are usually found near shore at all times until a size of at least 100 mm is reached. The above tests apply only to adult fish.

The distribution of 78 tag returns during the period June to November up to one year after tagging is shown in Figure 1, and the returns of 60 tagged fish during the period November to June up to one year after tagging is shown in Figure 2. Similar results were obtained for an additional 104 fish taken between 365 and 730 days at large during both periods.

It is clear from Figures 1 and 2 that winter flounder do not behave similarly during these two periods. The fish appear dispersed during the summer period, and most of the fish are found on the breeding grounds during the winter. Figure 1 does not convey a strong impression of directed movement, but it seems desirable to examine the dispersal phenomenon further.

A χ^2 test for similar proportions of returns from columns 2 and 4 of Table 2 gives the following results (χ^2=7.45, d.f.=5, P~.20). This information is used to indicate that the distribution of the tagged fish captured during 1958 was not significantly different from that of untagged fish in the major fishing areas when four or more individuals were caught.

Tag returns from other areas were not amenable to the statistical analysis because corresponding catch data were not available. The 17 additional tag returns from other areas during 1958 which provided accurate information on the place of recapture included seven recaptures from the vicinity of Charlestown Pond, Rhode Island, which is adjacent to the tagging site. The other 10 recaptured fish included two from Gayhead, Massachusetts, one from Vinyard Sound, Massachusetts, one from the vicinity of Nan-

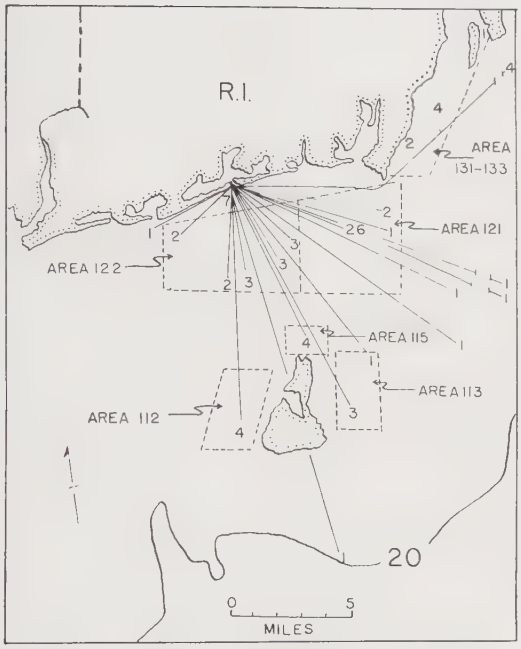

FIG. 1. Distribution of 78 winter flounder recaptured during June to November for a period of less than 365 days at large.

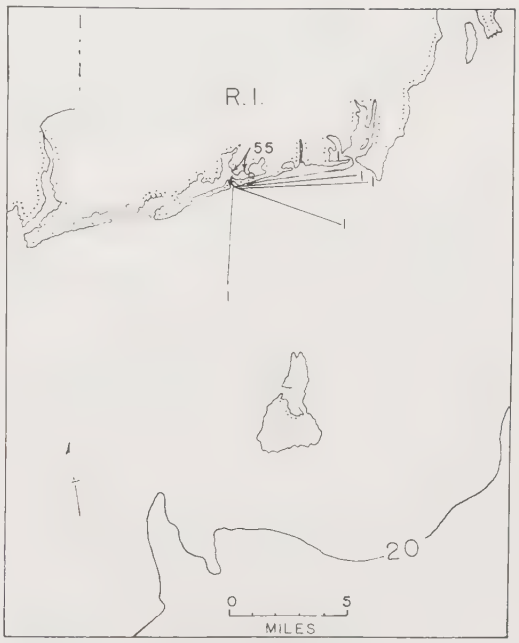

FIG. 2. Distribution of 60 winter flounder recaptured during November to June for a period of less than 365 days at large.

tucket Island, Massachusetts, one from Weekapaug Pond, Rhode Island, four from the Newport area, and one from south of Block Island.

A quantitative interpretation of Figures 1 and 2 is possible using the method of tag return analysis developed by Jones (1959). The formulae derived for estimating V, the directional component of the fishes' velocity, and a^2, the dispersion coefficient, are:

$$V = \frac{\Sigma r \cos \theta}{\Sigma t}$$

and

$$a^2 = \frac{1}{n}\left[\Sigma \frac{r^2}{t} - \frac{(\Sigma\, r \cos \theta)^2}{\Sigma t}\right]$$

where, for each recapture:

r = apparent straight-line distance travelled,

t = number of days at large,

θ = direction of travel measured from the axis of the coastline,

n = number of recaptures.

Estimates of the directional component of movement (V) and the dispersion coefficient (a^2) from available data are shown in Table 4. Comparison of the directional and non-directional components during the periods of less than and greater than one year at large shows remarkable similarity. Three hundred and sixty-five days have been subtracted from each recovery period in the 365–730-day recovery data. It is clear from these data that winter flounder return to the locality of tagging with high frequency.

The observed values of V are positive and they average .03 and .001 mile per day for the two periods under consideration. Positive values of V imply a mean displacement of fish to the east. The positive signs for these coefficients of directional movement are explained by the manner in which the angle θ was measured. Since these angles were measured in an east-to-west direction from the axis of the coastline, the relatively high catch and correspondingly high tag returns from code area 121 (east of the tag release point) provided many angles of less than 90°. These, of course, have positive values of cos θ. Available information on the total effort by major fishing areas (Col-

TABLE 4. *Estimates of* V *and* a^2 *from available tag-return data*

Period	Number of fish	Directional component miles/day	Dispersion coeff. miles^2/day
1. June–Nov (365 days at large)	78	.029	.670
2. June–Nov (365 days at large*)	32	.033	1.10
3. Nov–June (365 days at large)	60	.0004	.030
4. Nov–June (365 days at large*)	72	.0024	.016

* Period 2 and 4 coefficients of directional movement and dispersion have been obtained by subtracting 365 or 730 from each recovery period under the assumption of an annual return to the breeding area by individual fish.

umn 3 of Table 2) indicates a relationship between total effort and the catch of tagged or untagged individuals. The correlation coefficients are 0.85 and 0.88 respectively. Although a directional component of movement to the east is demonstrable from these data, it is suggested that it may be due to the unequal distribution of the catch and the related fishing effort.

Estimates of the dispersion coefficient a^2 are shown for available data in the last column of Table 4. These refer to the amount of undirected movement of fishes relative to one another during each period. The figures obtained in this study (1.1 and .67 miles^2 per day) compare favorably with a value of 1.5 miles^2 per day calculated for plaice by Beverton and Holt (1957). However, these values are considerably lower than those obtained by Jones (1959) for haddock. As with the directional component of movement, the non-directional component is consistently smaller during the cooler period of the year. This is thought to be associated with the smaller dimensions of the inshore environment.

The greatest apparent straight-line distance from release site to tag-recovery site was about 54 miles. The average apparent straight-line distance from tagging site to recovery area was 10 miles. The distances of tag recaptures from the original tagging site are comparable to those reported in a previous flounder study by Perlmutter (1947). The data at hand also support Perlmutter's statement that a winter flounder fishery is sustained by products of local spawning due to the fact that most observed movements have been restricted to relatively short distances. However, the magnitude of the contribution from particular breeding areas is not known at present.

It is conjectured that reassembly at the breeding grounds prior to and during the breeding season may be similar to diasporic migration defined by Wilkinson (1952). Gerking (1959), in a comprehensive summary of the movements of fish populations, states that probably no single mechanism will account for the homing response of fishes. The above is believed to be true in this instance also. However, since his survey made no mention of random searching it seems proper to examine this crude but perhaps logical method by which shallow water and the vicinity of the breeding grounds may be reached. Riley's (1956) investigation of Long Island Sound revealed only a weak and variable current in the vicinity of most tag recaptures, so it does not appear reasonable to postulate orientation to currents. Further, neither this investigation nor the investigations of the movements of marine demersal fishes summarized by Gerking (1959) provide information on other guiding mechanisms.

As mentioned previously, an idealized case is established where winter flounder are dispersed uniformly over a strip of ocean of width w bounded on one side by a depth contour which constitutes a reflecting barrier, and the other side contains the coastline which retains the fish on its arrival. It is assumed that, once the vicinity of the shore has been reached, winter flounder will search randomly along a narrow strip until an inlet is located by olfactory perception or some other means.

The width w of the bounded portion of the ocean is taken to be 15 miles. This distance coincides roughly with the presence of the 20-fathom contour beyond which tagged fish were not reported. Consider a random search for the coastline beginning at time zero. The percentage returning as a function of time is required under the assumption of random search. The empirical values of the coeffi-

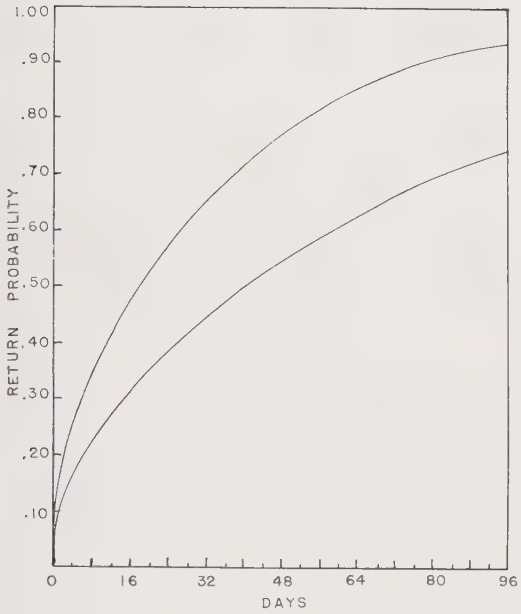

FIG. 3. Return probability in diasporic migration as a function of time, for $w=15$ and 10 and $a^2=1.1$.

cient of disperson $a^2=1.1$ miles^2 per day and $w=15$ miles are used. The fraction of fish still searching at time t can be obtained from:

$$\frac{2}{w^2} \sum_{n=1}^{\infty} \frac{1}{\alpha_n^2} e^{(-a^2\alpha_n^2 t)}$$

Derivation of the above is given in the appendix and is similar to the equation derived independently by Wilkinson (1952) for diasporic migration.

Figure 3 shows the return probability plotted as a function of time of search using two boundary widths. Similar calculations using a boundary width of 10 miles were also made because the majority of the fish were recaptured within this apparent straight-line distance from the point of release. It is evident from this figure that approximately 75% returns to shore are achieved after 90 days of searching in the case of the maximum strip width of 15 miles. If we assume a reflecting barrier at 10 miles, the return probability is more than 90% after 90 days of searching. These results are considered reasonable since the search period of 90 days lies within the time that winter flounder were actually observed to enter Green Hill Pond, and this period is less than the observed breeding season. Diasporic migration with no assumptions about orientation to outside stimuli seems a reasonable explanation for movement back to the coast.

APPENDIX

Grateful acknowledgment is made to Professor R. H. Goff, Mechanical Engineering Department, University of Rhode Island, for this derivation.

The random movement of fishes is considered to be approximated by the heat diffusion equation,

$$K\frac{\delta^2\phi}{\delta x^2} = \frac{\delta\phi}{\delta t}$$

with the boundary conditions ($x=0, \frac{\delta\phi}{\delta x}=0$ for reflection by the depth contour and $x=w$, $\phi=0$ for absorption by the coast). We start with the initial condition ($t=0, \phi=\phi_0$). Assume $\phi = X(x)T(t)$

$$KT\frac{d^2X}{dx^2} = X\frac{dT}{dt}$$

$$\frac{1}{X}\frac{d^2X}{dx^2} = \frac{1}{KT}\frac{dT}{dt} = -\alpha^2, \quad \frac{d^2X}{dx^2} + \alpha^2 X = 0$$

$$X = A_1 \cos \alpha x + A_2 \sin \alpha x$$

$$\frac{dT}{dt} + \alpha^2 KT = 0, \quad T = B_1 e^{-K\alpha^2 t}$$

Since $\phi = XT$

$$\phi = e^{-K\alpha^2 t}\,[C_1 \cos \alpha x + C_2 \sin \alpha x]$$

for $\frac{\delta\phi}{\delta x} = 0$, when $x = 0, C_2 = 0$

hence $\phi = Ce^{-K\alpha^2 t} \cos \alpha x$

for $\phi = 0$ when $x=w$ $\alpha = \frac{\pi(2n-1)}{2w}$ $n=1,2,3,\ldots$

Then $\phi_n = C_n e^{-K\alpha^2 t} \cos \alpha_n x$ where $\alpha_n = \frac{\pi(2n-1)}{2w}$

for $\phi = \phi_0$ when $t = 0$ we must use $\phi = \Sigma\phi_n$

$$\phi_0 = \sum_{n=1}^{\infty} C_n \cos \alpha_n x = \sum_{n=1}^{\infty} C_n \cos \frac{(2n-1)\pi}{2w} x$$

Multiplying both sides by $\cos \frac{(2K-1)\pi}{2w} x dx$ and integrating from $0 \rightarrow w$

$$\int_0^w \phi_0 \cos\frac{(2K-1)\pi}{2w}\,xdx = \sum_{n=1}^{\infty} C_n \int_0^w \cos\frac{(2n-1)\pi}{2w}\,x\cos\frac{(2K-1)\pi}{2w}\,xdx$$

$$= 0,\ K \neq n$$

$$= \frac{w}{2},\ K = n$$

$$\phi_0 \frac{2w}{(2n-1)\pi}\sin\frac{(2n-1)\pi}{2w}\,x\Big|_0^w = C_n\frac{w}{2}$$

$$\phi_0 \frac{2w}{(2n-1)\pi}(-1)^{n+1} = C_n\frac{w}{2},$$

$$\phi_0 \frac{1}{\alpha_n}(-1)^{n+1} = C_n\frac{w}{2}$$

$$C_n = \frac{2\phi_0}{w}\frac{1}{\alpha_n}(-1)^{n+1}$$

$$\phi = \frac{2\phi_0}{w}\sum_{n=1}^{\infty}\frac{(-1)^{n+1}}{\alpha_n}\,e^{-K\alpha_n^2 t}\cos\alpha_n x$$

To find total at time "t" we must find $\int_0^w \phi dx$

$$\int_0^w \phi dx = \frac{2\phi_0}{w}\sum_{n=1}^{\infty}\frac{(-1)^{n+1}}{\alpha_n}\,e^{-K\alpha_n^2 t}\int_0^w \cos\alpha_n x dx$$

$$= \frac{2\phi_0}{w}\sum_{n=1}^{\infty}\frac{(-1)^{n+1}}{\alpha_n}\,e^{-K\alpha_n^2 t}\left|\frac{1}{\alpha_n}\sin\alpha_n x\right|_0^w$$

$$= \frac{2\phi_0}{w}\sum_{n=1}^{\infty}\frac{(-1)^{n+1}}{\alpha_n^2}\,e^{-K\alpha_n^2 t}(-1)^{n+1}$$

$$= \frac{2\phi_0}{w}\sum_{n=1}^{\infty}\frac{1}{\alpha_n^2}\,e^{-K\alpha_n^2 t}$$

Total at $t = 0 = \phi_0 w$

The fraction at time "t" $= \frac{2}{w^2}\sum_{n=1}^{\infty}\frac{1}{\alpha_n^2}\,e^{-K\alpha_n^2 t}$

Substitution of a^2 for K gives the form described in the body of the report.

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COMPETITION BETWEEN *EUCYCLOPS AGILIS* AND *DAPHNIA PULEX*[1]

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ABSTRACT

Daphnia pulex suppressed the population development of *Eucyclops agilis* in mixed cultures. It appears that this reduced reproductive rate was due to the presence of *Daphnia* and not to metabolic products.

INTRODUCTION

In an earlier work it was shown that *Simocephalus vetulus* had a depressing effect on the number of *Cyclops viridis* occupying the same culture (Parker 1960). Reports by Fryer (1957a, 1957b) indicate that *Cyclops viridis* is predatory; among 51 guts examined he found approximately 22% with oligochaetes, 18% with cyclopoid copepods, 16% with dipteran larvae, and 6% with cladocerans. These figures suggest that the results obtained with *C. viridis* and *S. vetulus* may have been atypical since the copepods were forced to exist on an unnatural diet. Another possibility is that not all of the animals used were *C. viridis* since only a few were sent away for taxonomic verification; nevertheless, Fryer states that in general the large cyclopoids are carnivorous so that if members of other large species were present it is likely that they too were naturally carnivorous. This criticism pointed to the need of further work with a known herbivorous copepod; consequently, *Daphnia pulex* and *Eucyclops agilis* were the subject of the study reported here. *Eucyclops agilis* guts (106) were examined by Fryer and he found 67% with diatoms, 49% with filamentous green algae, and 32% with unicellular algae and broken colonies.

METHODS

Fundamentally the questions to be considered are two, 1) will *Daphnia pulex* suppress the *Eucyclops agilis* population and, if so, 2) how is this brought about; is competition direct or indirect? Toward these ends 180 cultures were established; 18 contained 1 gravid daphnid, 18 contained 1 gravid cyclopoid, and 144 contained 1 gravid daphnid and 1 gravid cyclopoid, in 50 ml of filtered lake water in every case. All cultures were kept under continuous light in a water bath at 20°C and were fed weekly with 1 ml of a suspension of *Chlamydomonas moewusii* having a Klett photometer reading of 150. This experiment ran for a period of 9 weeks and there were 10 treatments among the 180 cultures. These 10 treatment groups are described below:

Group	Treatment
0[1]	Pure *Daphnia*
0	Pure *Eucyclops*
I	*Daphnia* removed from mixed cultures after 1 week
II	*Daphnia* removed from mixed cultures after 2 weeks
III	*Daphnia* removed from mixed cultures after 3 weeks
IV	*Daphnia* removed from mixed cultures after 4 weeks
V	*Daphnia* removed from mixed cultures after 5 weeks
VI	*Daphnia* removed from mixed cultures after 6 weeks
VII	*Daphnia* removed from mixed cultures after 7 weeks
VIII	*Daphnia* removed from mixed cultures after 8 weeks

Two cultures were terminated weekly from each group and the copepods were counted in three categories: nauplii and copepodids with and without egg sacs. If a suppression of *Eucyclops* occurred and was due primarily to the physical presence of *Daphnia*, one would expect that the *Eucyclops* populations would respond promptly after the removal of *Daphnia*.

[1] This research was supported in part by a National Science Foundation Research Grant (G-8911).

TABLE 1. *Mean total number of* Eucyclops agilis *according to group (number of weeks with* Daphnia pulex*) and week*

Group	Week 1	2	3	4	5	6	7	8	9	Diagonal mean
0	1.0	1.5	7.5	9.5	19.5	10.5	74.0	85.0	77.0	77.0
I	5.0	3.0	2.5	3.0	0.5	24.5	22.5	8.5	37.0	56.0
II	2.5	4.0	0.5	3.0	8.5	12.5	27.0	21.5	38.0	40.2
III	4.5	0.5	3.0	4.0	4.0	7.0	34.5	1.0	58.0	28.1
IV	7.5	1.0	4.5	3.5	6.5	22.0	6.0	8.0	27.5	19.9
V	1.5	3.0	1.5	1.5	3.0	5.5	4.0	2.0	19.5	14.1
VI	2.5	1.5	1.0	5.5	0.5	3.5	2.5	1.0	3.5	5.5
VII	1.5	9.0	3.5	1.5	5.5	4.0	1.5	20.5	17.5	6.9
VIII	9.0	2.5	2.0	4.5	1.5	1.5	2.5	2.5	0.5	4.9
IX	4.4	3.1	2.5	3.3	2.8	3.0	2.0	2.5	—	

RESULTS

Before discussing the *Eucyclops* data, it should be noted that there was no significant difference between the mean number of *Daphnia* in pure culture and the mean number in mixed culture. As a result no effect of *Eucyclops* on *Daphnia* can be assumed nor will the possibility be considered further. Mean total numbers of *Eucyclops* are given by group and by week in Table 1. Group IX represents the mean of the weekly mixed culture means. It is obvious that the numbers of *Eucyclops* in group 0 are considerably higher than the numbers in group IX. In fact the numbers in group 0 appear to rise exponentially to a maximum near week 8 whereas the numbers in group IX are essentially constant or may be decreasing slightly. It would seem that in group IX, the numbers increased sharply from 1.0 during the first week due to the lack of daphnid influence on the forming of the egg sacs present at the start of the experiment. After the initial surge, the population essentially maintained its position at week 1. As for groups I–VIII, there is a great deal of variability; however, the general trend toward an increase in population size after the removal of *Daphnia* is apparent.

If groups 0–VIII are behaving reproductively alike one probably would conclude that the limiting effect of *Daphnia* was a direct one. Table 2 shows the total number of nauplii, copepodids, and copepodids with egg sacs for groups 0–VIII. A homogeneity χ^2 of 18.27 with 16 d.f. ($P<0.25$) supports the hypothesis that the relative abundances of the three development stages are the same for all groups. This leads one to compute the means for the diagonals involving only cultures without *Daphnia*. These figures provide a general picture of the population growth without the interference of *Daphnia* and can be compared with the corresponding values for group IX. The diagonal means

TABLE 2. *Total numbers of nauplii, copepodids, and copepodids with egg sacs, for each* Eucyclops *group after removal of* Daphnia

Group	Nauplii	Copepodids	Copepodids with egg sacs
0	160	380	31
I	56	137	10
II	80	128	14
III	49	156	12
IV	47	83	10
V	21	38	3
VI	3	10	1
VII	23	45	8
VIII	0	1	0

show essentially the same exponential picture as we noted for group 0.

Another check on the relatively low reproduction among the mixed cultures is obtained by comparing the totals (439 nauplii, 978 copepodids, and 89 copepodids with egg sacs) for groups 0–VIII combined (after removal of *Daphnia*) with the corresponding values for group IX. This comparison results in an unrealistic picture, since the first week totals for group IX are based on 16 cultures. These essentially all had the original adult present so that the adult category was weighted unduly. On the other hand, the first week totals for cultures without *Daphnia* are represented by only 2 cultures. Since groups 0–VIII have only 2 cultures per week per group, it would be better to use only 2/16 of the first week totals for mixed cultures, 2/14 for the second week, 2/12 for the third week, *etc.* Summing these values over all weeks gives 12.6 nauplii, 26.5 copepodids, and 7.5 copepodids with egg sacs. A value for χ^2 of 8.05 with 2 d.f. ($P<0.025$) points to a dearth of nauplii and copepodids relative to the copepodids with egg sacs.

Although the foregoing results suggest a direct interference by *Daphnia* with *Eucyclops* reproduction, additional support is necessary. In another experiment 8 lucite units were constructed, each consisting of 2 cylinders, 3 in. long by 2 in. in diameter, closed at one end. These were held together at the open ends by a metal bracket in such a way that an HA millipore filter (pore diameter $0.45\mu\pm0.02\mu$) was securely positioned between them. Two ¼-in. holes were drilled through the walls of each cylinder for the admission of water, food, and animals. One hundred milliliters of filtered lake water was placed in each side of the 8 units. Six units received 1 gravid *Eucyclops* on one side and 1 gravid *Daphnia* on the other. One unit received a *Daphnia* on each side and one unit received a *Eucyclops* on each side. Food was supplied at the same rate as in the previous experiment and the temperature was 20°C. Periodically all units were agitated gently so that diffusion of suspected inhibitory metabolites would be facilitated. Cultures were maintained for a period of 9 weeks after which all were terminated and the animals counted. Results for *Eucyclops* are presented in Table 3. Clearly the variability is excessive. However, there does not seem to be any real indication of population suppression among the *Eucyclops* grown with *Daphnia* on the other side of the millipore filter. In fact, the mixed cultures had a significantly higher proportion of nauplii and copepodids with egg sacs than did the pure cultures ($\chi^2=34.71$ with 2 d.f.). The mean total number of animals in the mixed cultures (69.8) agrees well with the total for group 0 after 9 weeks (77.0) as seen in Table 1.

TABLE 3. *Total and mean numbers of nauplii, copepodids, and copepodids with egg sacs for the pure* Eucyclops *culture and the 6 mixed cultures after 9 weeks*

Culture no.		Nauplii	Copepodids	Copepodids with egg sacs
1 (Pure)		21	69	0
		2	80	0
	Mean	11.5	74.5	0
2 (Mixed)		35	88	0
3 (Mixed)		22	25	11
4 (Mixed)		7	13	0
5 (Mixed)		32	155	4
6 (Mixed)		2	8	1
7 (Mixed)		0	13	3
	Mean	16.3	50.3	3.2

In summary, *Daphnia pulex* suppressed the population of *Eucyclops agilis* grown with it under laboratory conditions at 20°C. Experimental evidence indicates that the reduced reproductive activity of the *Eucyclops* is due to the physical presence of *Daphnia* and not to accumulated daphnid metabolic products.

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ON THE HYDROGRAPHY OF THE ST. ANDREW BAY SYSTEM, FLORIDA[1]

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ABSTRACT

The St. Andrew Bay System consists of four coastal plain estuaries of positive type. Temperature, salinity, and currents were observed over 24 hr for five to seven stations in the estuaries which were occupied five times in different seasons. At the two innermost stations, in the northern estuaries, the influence of drainage is strongest and the average salinity is low. There is almost no seasonal trend in average salinity or in the stratification of temperature and salinity. Tidal currents in the bays are predominantly diurnal, corresponding to tidal waves which enter the central bay through two passes. Surface currents often indicated longer duration of ebb than of flood stage, owing to the effect of drainage. Salinity change at the surface and bottom is caused primarily by the advective effect of currents, while in the mid-depths, salinity change is mainly due to the vertical motion of the halocline. At some stations, surface salinity showed a trend of continual decrease during 24 hr, instead of a periodic change owing to persistent ebb currents. Bottom salinity, however, usually changed periodically or was almost constant, even at these stations. In one survey, surface salinity showed a trend of increase, owing to persistent flood currents caused by winds. Salinity change at a station in a narrow pass was most sensitive to change of currents. An equation which postulates that the change of salinity during one tidal period is proportional to mean horizontal gradient of salinity and mean current is tested by several examples. Vertical stability is largest at two innermost stations and shows no seasonal trend, as is often observed in other estuaries and in the open sea.

INTRODUCTION

The St. Andrew Bay System consists of a group of coastal plain estuaries on the northern Gulf coast of Florida included within the area bounded by Long. 85°23′ to 85°53′ W and Lat. 30°00′ to 30°20′ N. The group of four bays covering some 90 sq miles consists of St. Andrew, West, North, and East bays (Fig. 1). The central portion, St. Andrew Bay, is the only one of the four bays which communicates directly with the Gulf, through West Pass to the south, and through the much larger East Pass to the southeast. North and West bays come together to form the upper arms of a "Y" before they open, at the base of the "Y," into St. Andrew Bay. East Bay opens into St. Andrew Bay, extends about 20 miles to the southeast, and heads in a small river.

Drainages into these bays are small but they are generally positive (Pritchard 1952) in estuarine classification (*i.e.*, evaporation is less than drainage inflow) except in St. Andrew Bay, where the salinity is almost equal to that of the open sea (a nearly neutral condition).

The bottom contours obtained from U. S. Coast and Geodetic Survey Charts 1263 and 869 are indicated in Figure 1. As is seen from this chart, the mean depth of St. Andrew Bay is the greatest and is about 17.0 ft. The other bays are of approximately the same mean depth; mean depths of East, North, and West bays are 7.0, 5.7, and 6.7 ft, respectively.

HYDROGRAPHIC DATA

Hydrographic and marine biological surveys of this area have been continued since 1957 by the Oceanographic Institute with cooperation from U. S. Navy Mine Defense Laboratory, Panama City, under the sponsorship of Office of Naval Research. Seven stations, shown in Figure 1, were occupied simultaneously for water sampling, tempera-

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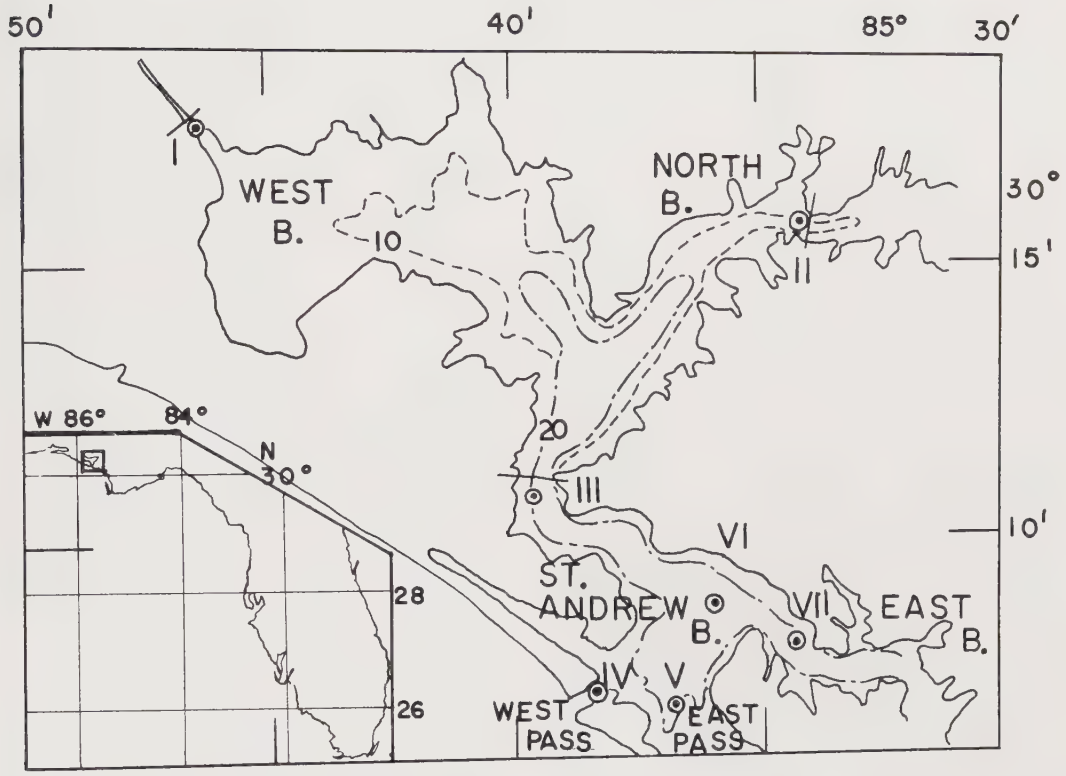

FIG. 1. The St. Andrew Bay System and location of seven survey Stations. (Contours of 10- and 20-ft depths are shown with broken and chain lines, respectively.)

ture and current measurements, and other observations at 1-hr intervals during 24 hr. Water samples were taken at the surface, mid-depth and bottom for each station. Temperature was measured with a bathythermograph and current data were obtained by the use of floats or Price Current meters. Such surveys were carried out five times since 1957, on 7 to 8 November in 1957, 27 to 28 March, 5 to 6 June, 18 to 19 September in 1958, and 19 to 20 February in 1959 (Jones and Ichiye 1960).

The average values and ranges of salinity and temperature over 24-hr periods, at the surface and bottom, are tabulated in Tables 1 and 2, respectively. In most cases temperature and salinity in mid-depths are intermediate between the values at the surface and the bottom.

General inspection of the data reveals that salinity fluctuations during a tidal cycle are particularly conspicuous at the surface of Stations I and II. It is seen from Table 1 that the range of salinity change is usually larger at the surface, except at Stations I and II, where the range of the bottom salinity was sometimes larger than that at the surface. The low average salinity at Stations I and II suggests that these stations are most influenced by drainage. It is to be noted that in the first and the fourth observations the range of salinity at these stations was exceptionally small, suggesting that the effect of tidal currents was slight on these occasions. Station IV represents the strongest oceanic influence, as seen from its high average salinity. There is almost no seasonal trend in salinity stratification, and even the data of June do not indicate so large a salinity difference between the surface and the bottom, as is usually observed in the sea.

Average temperature at each station shows seasonal change. However, fluctuations during 24-hr periods are slight and

TABLE 1. *Average salinity and range of salinity change. In the depth column, S indicates surface. Only surface and bottom data are shown. Average salinity and ranges of salinity change during 24 hr (in brackets) are indicated in parts per thousand.*

Station	Depth (in ft)	Surveys with dates 1st: 7–8 Nov, 1957	2nd: 27–28 Mar, 1958	3rd: 5–6 June, 1958	4th: 18–19 Sept, 1958	5th: 19–20 Feb, 1959
I	S	22.6 (9.7)	5.1 (8.5)	16.8 (1.2)	22.0 (1.1)	3.9 (4.5)
I	8–12	26.7 (3.6)	14.7 (19.3)	17.7 (3.4)	22.7 (2.0)	20.8 (22.7)
II	S	16.7 (12.8)	8.3 (10.9)	9.7 (6.3)	9.9 (11.4)	—
II	16–18	30.3 (1.8)	25.0 (10.7)	25.8 (1.3)	26.3 (2.0)	—
III	S	27.1 (6.1)	20.9 (1.8)	—	25.9 (1.8)	—
III	40–44	32.5 (1.9)	33.1 (2.4)	—	30.3 (1.5)	—
IV	S	32.8 (3.5)	29.9 (10.4)	28.7 (7.9)	29.9 (3.9)	29.5 (8.3)
IV	40–45	33.3 (3.3)	34.2 (4.5)	30.0 (5.9)	31.2 (2.4)	33.0 (7.0)
V	S	31.1 (3.9)	26.0 (3.6)	23.6 (6.9)	28.3 (2.3)	28.0 (1.8)
V	50–55	33.2 (3.0)	34.1 (1.4)	30.0 (1.7)	31.0 (3.1)	29.5 (7.3)
VI	S	30.5 (1.4)	25.0 (1.4)	21.3 (6.2)	28.3 (2.2)	—
VI	40–45	34.2 (0.8)	34.3 (2.7)	30.5 (0.9)	31.3 (1.0)	—
VIII	S	28.5 (1.2)	25.1 (2.6)	28.8 (5.3)	27.7 (5.2)	27.2 (1.3)
VII	40–44	34.1 (2.4)	34.5 (1.0)	29.6 (4.2)	30.7 (2.2)	33.5 (0.5)

quite irregular, compared with salinity fluctuations, owing to the influence of surface heating and cooling in addition to tidal currents. Difference of temperature between different stations is small and there is no characteristic difference in temperature and its fluctuations, between Stations I and II and other stations as is the case in salinity fluctuations. Vertical difference of temperature at each station is also small, even in summer when a thermocline develops usually in the sea.

Surface current measurements were made during the third and fourth surveys, and these are tabulated in Table 3, in which the direction, maximum velocity, and time of onset of flood and ebb current, at the surface, are shown for each survey.

The tidal currents at all stations are predominantly diurnal, corresponding to the tides of the bays. Tidal waves enter the Bay System mostly through East Pass (Fig. 1) and advance to the inner ends of the Bay System. From one-half to one-third of the volume passing through East Pass flows through West Pass. High and low water times at each station, estimated from the Tide Tables of the Coast and Geodetic Survey, indicate that

TABLE 2. *Average temperature and ranges of temperature change. S indicates surface; B, bottom. See Table 1 for depths. Average temperature and ranges of temperature change during 24 hr (in brackets) are indicated in °C.*

Station	1st	2nd	3rd	4th	5th
I S	20.7 (2.4)	16.7 (1.0)	29.5 (1.6)	27.2 (2.0)	16.1 (1.9)
I B	20.6 (1.2)	16.7 (1.1)	29.3 (1.5)	27.2 (1.9)	—
II S	20.5 (1.9)	16.3 (3.3)	28.7 (3.9)	28.9 (2.3)	—
II B	20.7 (2.0)	16.0 (3.9)	28.3 (3.8)	29.2 (0.6)	—
III S	20.3 (2.2)	16.2 (1.9)	—	27.9 (1.1)	—
III B	21.6 (1.0)	15.8 (1.0)	—	27.9 (2.0)	—
IV S	21.5 (2.1)	16.3 (1.0)	28.8 (1.2)	28.7 (1.5)	15.2 (1.1)
IV B	21.7 (2.1)	16.4 (1.1)	28.7 (1.5)	28.5 (1.3)	—
V S	21.4 (1.6)	15.9 (1.0)	28.5 (1.6)	27.9 (1.5)	16.0 (1.6)
V B	22.1 (0.7)	16.1 (1.2)	28.7 (1.6)	28.0 (0.6)	—
VI S	21.2 (0.3)	16.2 (0.7)	28.6 (1.9)	28.3 (1.6)	—
VI B	22.4 (0.6)	16.5 (0.4)	28.7 (2.2)	28.5 (1.7)	—
VII S	20.6 (0.8)	16.4 (0.7)	28.1 (2.1)	28.1 (1.1)	16.5 (0.9)
VII B	22.3 (0.3)	16.2 (1.2)	27.9 (1.6)	27.9 (1.1)	—

TABLE 3. *Characteristics of surface currents*

		Sta. I	Sta. II	Sta. III	Sta. IV	Sta. V	Sta. VI	Sta. VII
Direction	Flood	NW	W	N	NE	WNW	NE-N	S-SE
	Ebb	SE	E	S	SW	ENE	SW-S	W-NW
				Third survey				
Max. Velocity (knots)	Flood	0.4	0.6	–	1.0	0.5	0.4	0.8
	Ebb	0.3	0.9	–	1.2	0.6	0.6	0.6
Onset of*	Flood	L+5	L−1	–	L−1	L+1	L+2	L+0
	Ebb	H+5	H+0	–	H+0	H+2	H+0	H+1
				Fourth survey				
Max.Velocity (knots)	Flood	0.5	–	0.4	1.0	–	0.5	0.5
	Ebb	0.8	–	0.6	1.2	–	0.6	0.6
Onset of*	Flood	L+7	L+3	L+3	L+1	L+3	L+3	L+1
	Ebb	H+4	H−2	H+1	H+1	H+3	H+0	H+1

* H+1 or L−2 indicates 1 hr after high water or 2 hr before low water respectively.

the arrival time of tidal waves at each station is later than at Station V, which is located at an inner end of East Pass. The estimated time lags in minutes are shown below:

Station	I	II	III	IV	V	VI	VII
High	113	89	50	4	0	25	60
Low	213	150	105	8	0	50	105

Table 3 indicates that current speed is strongest, with a maximum of more than one knot, at Station IV, which is located in narrow West Pass. Ebb or flood currents begin at approximately high water or low water at each station, except at Station I. This station is so little influenced by the tidal waves coming from the open sea, that time lags of currents from tidal heights may be from 5 to 7 hr.

In most cases, the duration of ebb currents is longer than that of flood currents, except for those at Station IV in the first survey which will be discussed later. This is apparently due to the effect of drainage, which causes a stationary outward current in the upper layer (Pritchard 1952).

Tidal ellipse of all stations, even though in a relatively broad channel, is almost rectilinear, except at Station VI. The tidal waves seem to depart in two directions near this station, where the main directions of currents were NE and SW at one tidal cycle and N and S at another. Therefore, in St. Andrew Bay, tidal currents change their direction in a short distance, and inertia terms become large owing to small curvature of the streamlines. For instance, the radius of curvature around Stations VII, VI, and V is equal to 1.4 naut. miles in ebb currents, with maximum velocity of about 0.6 knot. The inertia term of (velocity)/(radius of curvature) was then equal to 1. 19×10^{-4} sec^{-1}, which is larger than Coriolis' coefficient 0.7×10^{-4} sec^{-1} (Stewart 1957).

SALINITY CHANGE DUE TO TIDAL CURRENTS

Salinity changes in this bay system are caused primarily by advection due to tidal currents. The equation for conservation of salinity is generally given by

$$\delta S/\delta t + u\,\delta S/\delta x = \text{Diffusion Terms} \quad (1)$$

where S is salinity, u is horizontal velocity, t is time, and x is distance. The x-axis is taken along the direction of maximum gradient of salinity and u is the velocity component in that direction.

When the diffusion terms of (1) are neglected and u is assumed to be periodic with time, the range of salinity change is proportional to $\overline{U}\,\delta\overline{S}/\delta x$ (Ichiye 1952), in which $\overline{U}$ is the amplitude of u and $\delta\overline{S}/\delta x$ is the horizontal gradient of the temporal average of salinity. The ranges of salinity of Stations I and II are plotted against the differences of time-averaged salinities between Station III and each of these stations in Figure 2A. A general linear relation, except some data of Station I, suggests that salinity change at these stations is caused primarily by advective effect of tidal currents.

On the other hand, the salinity change at the mid-depth is considered to be caused mainly by the vertical motion of the halo-

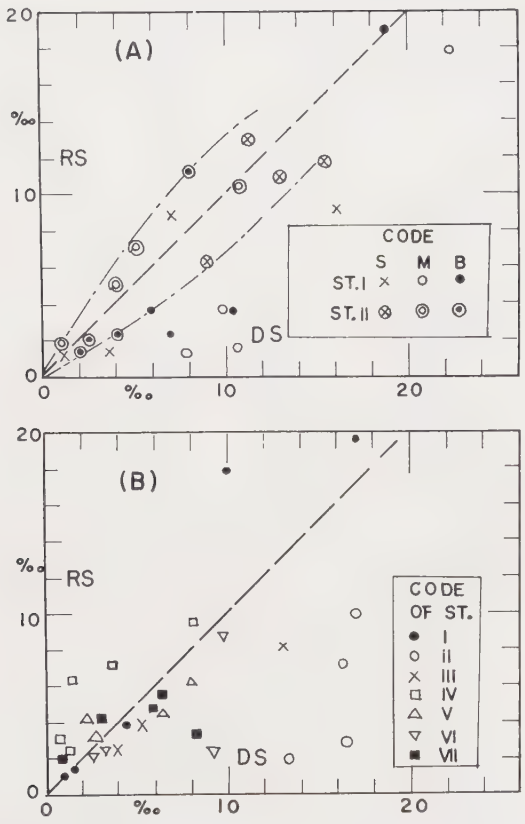

FIG. 2. Relationships between range of salinity change during 24 hr, and horizontal and vertical differences of mean salinity. (A) Range of salinity change (RS) at Stations I and II against horizontal difference of salinity (DS) between Station III and Station I or II. In the code, S, M, and B are surface, mid-depth, and bottom, respectively. (B) Range of salinity change at mid-depth (RS) against difference of mean salinity between bottom and surface (DS) at each station.

cline. In order to confirm this assumption, the range of salinity change at the mid-depth has been plotted against the difference of time-averaged salinity between the bottom and the surface, in Figure 2B for each station. Most of the points are near or below a line at an angle of 45° to the ordinates, except two points for Stations I and IV. The exceptional point of Station I suggests that the salinity change on this occasion was also influenced by the tidal currents, since, in Figure 2A this point is in good agreement with the linear relation formed by other points.

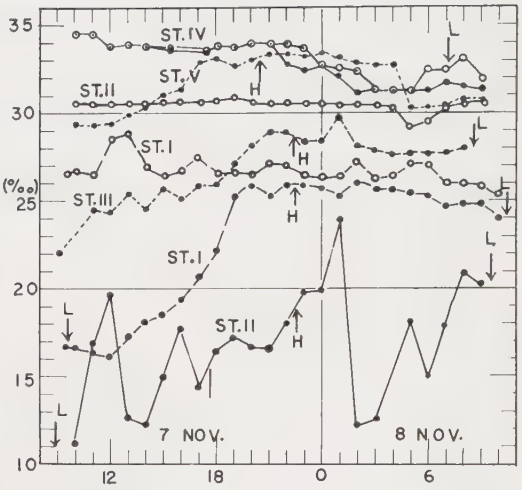

FIG. 3. Salinity change at Stations I, II, III, IV, and V in the first survey (7 to 8 November, 1957). Surface and bottom salinities are indicated by closed and open circles, respectively. High and low water stages at each station are indicated by arrows with letters H and L, respectively.

SALINITY CHANGES IN EACH SURVEY

Although salinity changes in this bay system may be, on the whole, caused by tidal currents, the mode of change is different at each station in each survey. In particular, surface salinity at some stations did not show a periodic change with the tides but indicated a trend of increase or decrease during 24 hr, owing to stationary currents caused either by drainage or surface wind drift.

First survey—Salinity change at Stations I to V is plotted in Figure 3. At Station I, surface salinity increased by about 10‰ from 1200 to 2000 on November 7, and remained almost the same thereafter. At Station II, surface salinity showed a trend of increase, although it suddenly decreased from 24.1‰ at 0100 to 12.3‰ at 0200 on November 8, and fluctuations of amplitudes of 1.5 to 4‰ with periods of about 4 hr were superposed on this trend. At Station III, a trend of increase of surface salinity is seen from 1000 to 2100 of the first day. Bottom salinity at these stations was almost constant (at Station II) or fluctuated slightly (Station I and Station III). At Station IV, salinity was almost uniform vertically and also constant with time, except a slight decrease from 2200 of the

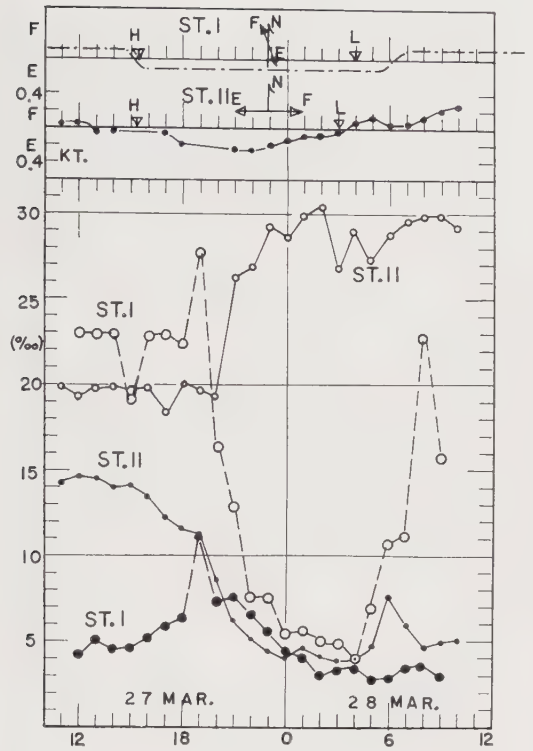

FIG. 4. Salinity and currents at Stations I and II. Current directions are indicated by arrows for ebb (E) and flood (F). For Station I directions of bottom current only are shown. For Station II, direction and velocity of surface currents are shown. Surface and bottom salinity are indicated by closed and open circles, respectively. Upper part, currents; lower part, salinity.

first day to 0200 of the next day. The trend of increase of surface salinity at Stations I, II, and III is apparently related to persistence of flood currents during the 24 hr which were actually observed at Station IV. In most other cases ebb current lasted longer than flood currents at the surface, owing to drainage. Meteorological data indicate that this persistence of northward currents may be attributed to prevailing southerly winds along the coast and/or to long waves generated at a stationary front which had persisted from November 6 in the northern Gulf and was located about 200 miles to the west of the Florida coast at 0100 of November 8 (Ichiye 1950). At Stations V, VI, and VII, change of salinity was slight both at the surface and bottom, except the surface salinity at Station V, which showed higher values at high water and lower values at low water.

Second survey—Salinity and current data at Stations I and II are plotted in Figure 4. Surface currents at Station I showed ebb current during the 24 hr but bottom currents, estimated by directions of the slope of a sounding wire, showed ebb and flood currents, corresponding to tides, as indicated in the figure. Therefore, surface salinity changed irregularly with small amplitudes of fluctuation, while bottom salinity showed a conspicuous decrease or increase after the shift of currents from flood to ebb or from ebb to flood respectively. At Station II the surface salinity showed a trend of decrease, which can be explained from the persistence of ebb currents till 0300 on March 28. The increase of salinity at the bottom after 0200 seems to be due to onset of flood currents which was earlier at the bottom than at the surface.

At Station IV, surface salinity was sensitive to change of currents because this station is directly influenced by water coming from the Gulf. Change of currents from flood to ebb at 1400 on March 27 caused the decrease of surface salinity from 35.3‰ at 1200 to 28.1‰ at 1400 and another change of currents from ebb to flood currents at 0500 caused the increase from 25.3‰ at 0300 on March 28 to 35.0‰ at 0600. It is noted that the salinity of Stations III, VI, and VII did not show any remarkable fluctuation.

Third survey—At Station I, salinity change with time and the difference of salinity at different depths were small, suggesting that the water at this station was well mixed vertically and horizontally. At Station II, surface salinity, which was between 7 and 10‰ from 1000 on June 5 to 0200 on June 6, increased to 11.8‰ at 0500. This increase lagged 4 hr behind the change of currents from ebb to flood at 2300. The salinity at the bottom was almost constant (about 26‰). Salinity and currents at Station IV are plotted in Figure 5A. As was the case in the second survey, salinity at Station IV was most sensitive to the change of currents. At the outset of ebb currents, the surface salinity began to decrease immediately, but the de-

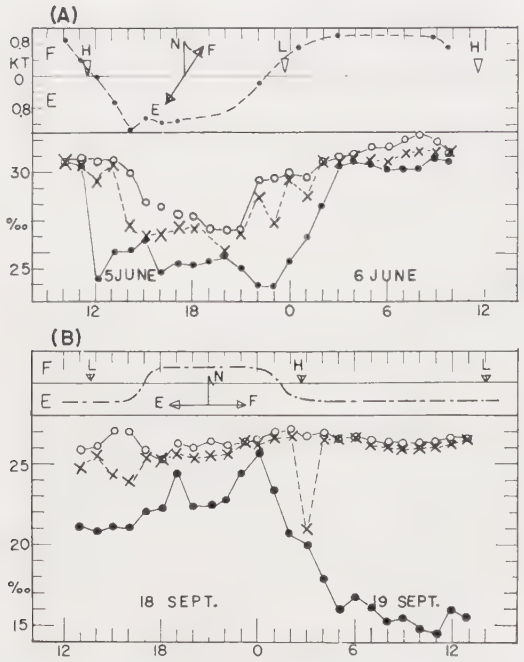

FIG. 5. Currents and salinity changes from the third survey at Station IV (A) and from the fourth survey at Station II (B). Upper part, surface currents; lower part, salinity. Surface, mid-depth, and bottom salinity are shown by closed circles, cross, and open circles, respectively. See legend of Figure 4.

crease of the bottom salinity began 2 hr later. On the other hand, at the onset of flood currents, the bottom salinity increased at once, but the increase of the surface salinity showed a time lag of 2 hr. This was due to the fact that ebb currents started earlier at the surface than at the bottom, but flood currents started earlier at the bottom, owing to the effect of drainage. The surface salinity at Station V decreased gradually from 27.5‰ at 1300 on the first day to 20.6‰ at 0300 on the second day and then increased by about 1‰ and remained at this level until 1000. At Station VI, surface salinity changed with tides, showing a maximum of 24.2‰ at high water and a minimum of 18.0‰ 2 hr after low water. At Station VII, surface salinity was almost constant, except at the mid-stage of ebb currents, when the salinity increased by 4‰ in 3 hr and then decreased to the initial level of about 18‰ in 2 hr. Bottom salinity of Stations V, VI, and VII was almost constant.

Fourth survey—Vertical gradient and ranges of salinity at all stations, except Station II, were smaller than other surveys, suggesting that salinity distributions were more homogeneous, both horizontally and vertically. At Station I, particularly, the salinity was constant with time and was vertically homogeneous. At Station II, surface salinity increased from 21.3‰ at 1300 on September 18 to 25.8‰ at midnight, decreased rapidly to 16.0‰ at 0500 and remained between 15 and 17‰ thereafter, while bottom salinity was almost constant (Fig. 5B). Stations III to VI showed a slight change of salinity at the surface with tides, with higher values at high water, while bottom salinity was almost constant, except at Station IV, where the bottom salinity-change with tides occurred with a lag of 3 hr after the change of surface salinity.

Fifth survey—Currents and salinity at Stations I and IV are plotted in Figure 6. At Station I, ebb currents continued at the surface from 1500 on February 19 until 1300 on the next day, while at the bottom, ebb currents lasted only from 2200 on February 19 to about 0900 on the next day. Surface salinity changed slightly with tides and showed higher values at high water than at low water. Bottom salinity, however, fluctuated by about 22‰ between 2300 and 0900, decreased after the shift of bottom currents from flood to ebb at 2300, and increased suddenly between 0800 to 1000 on February 20, apparently due to shift of bottom currents from ebb to flood. This sudden change indicates that a sharp salt wedge was formed near the bottom. At Station IV, surface ebb currents reached 2 knots. Bottom currents were weak and changed from flood to ebb with a lag of 3 hr behind the shift of the surface currents. Salinity changes reflected the change of currents and, at shift of currents from flood to ebb, surface salinity decreased 3 to 4 hr earlier than the bottom salinity. The increase of bottom salinity at 0300 indicates that shift from ebb to flood was earlier at the bottom than at the surface.

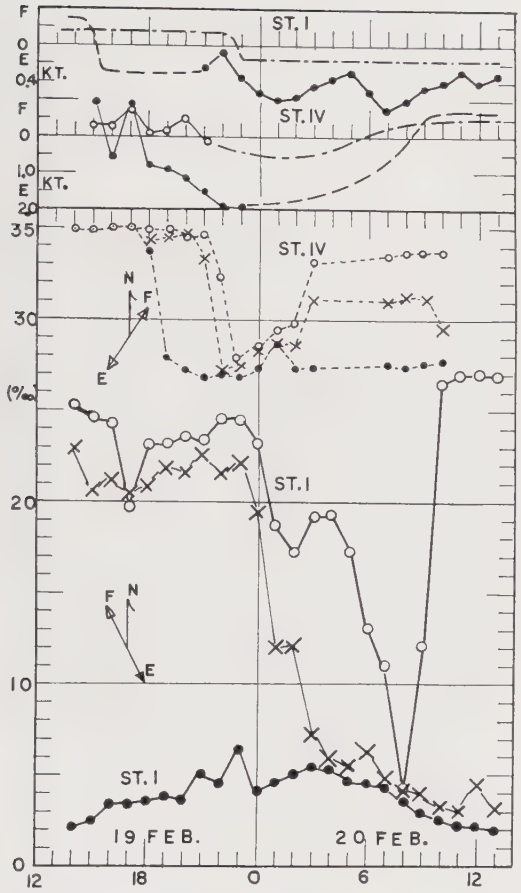

FIG. 6. Currents and salinity at Stations I and IV from the fifth survey. Upper part, currents; lower part, salinity. Estimated currents at the surface and bottom are shown by broken line and chain line, respectively, and their directions only are indicated in the figure. See legend of Figure 4.

TREND OF SALINITY CHANGE IN AN ESTUARY

Salinity of some stations indicates a trend of decrease or increase during 24 hr as discussed in the preceding section. This trend was explained as the effect of constant drainage superposed on tidal currents. A mathematical model of this problem will be treated.

As a basic equation of salinity change, equation (1), without a diffusion term, is considered. Velocity u and the horizontal gradient of salinity $\delta S/\delta x$ are assumed to consist of a constant and periodic term with time, such as

$$u = \overline{U} + v \cos (2\pi t/T + m) \qquad (2)$$

$$\delta S/\delta x = C + c \cos (2\pi t/T + n) \qquad (3)$$

Substituting (2) and (3) into (1) (without a diffusion term) and integrating with time over one period T, we have an increase or decrease of salinity during T given by

$$D = S(T) - S(0) = \overline{U}CT + \tfrac{1}{2}vc \cos (m - n) \qquad (4)$$

The phase of a periodic term of $\delta S/\delta x$ is almost equal to that of S. Generally c in the equation (3) is much smaller than C. Also most examples of 7 stations indicate that $m - n \approx \pm \pi/2$. Therefore we may put, with good approximation

$$D = \overline{U}CT \qquad (5)$$

This relation will be verified with several data.

1) *Stations I, II, and III of the first survey (Fig 3):* Salinity of these stations showed a trend of increase. At Station I, $D = 8.3‰$ and $C = 4.6‰$ per 9.0 naut. miles (decrease from Station III to Station I). Thus equation (5) gives $U = 0.67$ knot (inward). For Station II, $D = 9.3‰$ and $C = 10.4‰$ per 8.0 naut. miles (decrease from Station III to Station II); thus, $U = 0.30$ knot (inward). For Station III, $D = 5.0‰$ and $C = 5.8‰$ per 3.2 naut. miles (decrease from Station IV to III); thus, $U = 0.12$ knot (inward). A source of errors in this estimation may be included in the crude method for C which is computed over a too long distance between two stations. Actual values of C should be higher than those obtained with this method, and, thus, actual values of U must be lower than those obtained. However, it seems to be significant that the mean velocities U increase from Station III to Station I or towards the inner end. This suggests to us that the possible mechanism of a trend of increase of salinity is caused by inflow from the open Gulf which increases its velocity towards the inner end, as a cross section of the bay decreases.

2) *Station II of the second survey (Fig. 4):* $D = 8.8‰$ (decrease). $C = 12.6‰$ per 8.0

TABLE 4. *Frequency of occurrence of salinity differences in parts per thousand per 5 ft taken from hourly data at Stations I and II, by stations and by surveys*

‰	0–1	1–2	2–3	3–4	4–5	5–6	6–7	7–8	8–9	9–10	10–11	11–15	15–21
Sta. I	45	15	2	3	0	1	4	4	3	2	1	6	2
Sta. II	1	4	10	7	8	9	17	7	15	17	4	0	0
Total	46	19	12	10	8	10	21	11	18	19	5	6	2
Cruise 1	10	4	1	1	1	3	6	6	5	8	3	0	0
Cruise 2	4	3	2	6	4	1	6	4	6	2	1	6	2
Cruise 3	9	4	1	1	3	1	4	1	7	9	1	0	0
Cruise 4	23	8	8	2	0	5	5	0	0	0	0	0	0

naut. miles (decrease from Station III to Station II). Thus, $U = 0.22$ knot (outward) from equation (5). The average of observed currents is equal to 0.07 knot (outward). A value of U for observed currents smaller than that obtained by computation is, again, due to the condition that C is underestimated by taking a distance too long.

3) *Station V of the third survey.* From the observed salinity change we have $D = 5.4$‰ (decrease). The average velocity observed over 24 hr gives $U = 0.044$ knot. From equation (5) we have $C = 5.1$‰ per naut. miles with $T = 24$ hr. The difference of time-averaged salinity between Station IV and Station V gives $C = 5.0$‰ per naut. mile, which is in good agreement with the value computed from (5). The mean current at Station V is towards Station IV (inward) and the mean salinity decreases from Station IV to V. Thus salinity at Station V showed a trend of decrease during 24 hr.

4) *Station II of the fourth survey (Fig. 5B):* $D = 5.6$‰ (decrease). $C = 1.0$‰ per naut. mile (decrease from Station III to Station II). The difference of time-averaged salinity between Stations III and II is equal to 8.0‰ and the distance is about 8.0 naut. miles. From equation (5) $U = 0.23$ knot. In this survey only current directions were observed, indicating 8 hr of flood and 16 hr of ebb currents. In the third survey the maximum velocity of flood and ebb currents was 0.4 and 0.9 knot, respectively. If these maximum velocities are assumed to be valid in this case, the mean current in knots is given by

$$\int_0^T u\,dt/T = (0.4\times 8 - 0.9\times 16)/(24\pi) = -0.15$$

which is not too far from the value computed with the equation (5) mentioned above. (Currents are assumed to change as a sine function of time.)

As illustrated in these examples, a model of salinity change in an estuary represented

TABLE 5. *Frequency of occurrence of salinity differences in parts per thousand per 10 ft taken from hourly data at Stations III to VII, by stations and by surveys*

‰	0–1	1–2	2–3	3–4	4–5	5–6	6–7
Sta. III	0	33	5	5	2	10	8
Sta. IV	66	16	11	4	2	0	0
Sta. V	18	31	9	11	12	9	7
Sta. VI	13	35	9	20	16	3	0
Sta. VII	4	32	16	22	17	6	0
Total	101	147	50	62	49	28	15
Cruise 1	39	54	20	5	1	0	0
Cruise 2	9	4	13	37	26	13	15
Cruise 3	13	14	16	20	22	15	0
Cruise 4	40	79	1	0	0	0	0

by equation (5) seems to be in good agreement with actual situations in St. Andrew Bay System. This gives further evidence that mixing of water is not complete during one tidal cycle in this bay system.

VERTICAL STABILITY

Vertical stability (hereafter called simply stability) in shallow waters is proportional to a difference of density *in situ* per unit vertical distance (Sverdrup, *et al.* 1942). Water temperature in estuaries is more uniform vertically than salinity, and stability may be represented by vertical gradient of salinity only.

The frequency distribution of the occurrence of maximum salinity differences has been determined for the hourly data. In Tables 4 and 5 the numbers of hourly data are shown against ranges of maximum salinity differences for each station and for each survey. The range of salinity difference is taken at one part per thousand of salinity per 5-ft depth for Stations I and II (Table 4), because sampling depths of these stations were at approximately 5-ft intervals. However, the range is taken at one part per thousand of salinity per 10-ft depth for Stations III to VII (Table 5), because sampling depths were taken at from 10- to 25-ft intervals. Casual inspection of the tables confirms that Stations I and II show a greater stability than Stations III to VII, as stated in the previous section. In fact, the average maximum salinity difference of Stations I and II is 4.9‰ per 5-ft depth, while this difference is only 2.4‰ per 10-ft depth for Stations III to VII. However, the most frequently occurring salinity difference at Stations I and II is in a range of salinity difference of 0 to 1‰ per 5 ft. This is mostly due to contributions of data from Station I in the fourth survey, in which fresh water was found almost to the bottom. Discarding these contributions, the maximum frequency of salinity differences is in ranges of 6 to 7 and 8 to 9‰ per 5 ft as is the case in Ochlockonee Bay (Ichiye, *et al.* 1960). It is to be noted that no seasonal tendency is recognized in frequency distributions of salinity differences. The stability is greatest in the second survey at all stations. This survey was carried out in March and not in warm seasons, and thus it would appear that stability in this bay does not depend upon surface heating, as is the case in the open sea.

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OBSERVATIONS ON INTERNAL WAVES IN SHALLOW WATER

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ABSTRACT

Observations made off the San Diego coast in 1959 are presented and discussed. Two different systems for recording temperatures were employed and thermistors were used in both of them. The transducer component of one consists of several thermistors by which temperature is measured at fixed depths. The other system includes a sea element which is automatically and continuously positioned on a selected isotherm. Ocean temperature was simultaneously recorded at three locations. Series of internal waves of relatively high frequency usually follow high or low tide and persist for approximately one hour. Single waves that are separated from other significant thermal disturbances and not related to any particular phase of tide progress in the same area. Profiles of both types of waves show that they are strongly influenced by boundary conditions. Wave displacement is upward when the thermocline is near the bottom and downward when the thermocline is higher. Internal tides are present throughout a 7-day record of isotherm depth. The phase relation between the surface tide and internal tide is variable over time but the period and asymmetry of the two waves are similar.

INTRODUCTION

For several years the Physical Oceanography Section of the Navy Electronics Laboratory has been making time-series observations of temperature in shallow water near San Diego, California. Data are taken to be used in numerical analysis of the various temperature phenomena which occur in the ocean. However, study of the data has revealed that some of the physical processes are repetitive enough to warrant special attention. This report is concerned with repetitive thermal processes associated with internal waves in shallow water.

This discussion deals with relatively high-frequency "internal waves" in which a loosely defined distinction is made between turbulent fluctuations and genuine internal waves. A maximum frequency, above which internal waves may be created but will not propagate, exists as a function of the density and density gradient. A rough estimate of this "cut-off" frequency (Vaisala frequency) is about 5 min for summer conditions off San Diego, consequently, thermal disturbances with periods less than 4 to 5 min are not considered in this report. However, the true value of the "cut-off" frequency varies with time and space and must be computed for each vertical density distribution. In this regard, the term internal waves is used here although reference to wave-like features might be more accurate. They are considered internal waves in the sense that the perturbations of temperature that characterize them have their greatest amplitudes at some level below the free surface. Their wave-like nature is exhibited by the periodic occurrence of the disturbances and their forward progression at speeds and along directions which are clearly identifiable. Thus wave-like features of period greater than about 5 min are found to progress as broad wave fronts within the body of the water depth and their directions of propagation deviate only slightly from a common mean. These waves are identifiable without the aid of statistical analysis over the distances of the triangular networks shown in Figure 1.

METHOD OF MEASUREMENT

Data on internal waves were collected by using temperature fluctuations as a measure of density fluctuations. This approach necessarily was taken because devices that measure density continuously *in situ* are not available. However, all the data were collected at one location where salinity measurements indicated that deviations from a vertically isohaline structure were small enough for the temperature to be an adequate index of density.

The duration of each set of observations usually was a multiple of diurnal tide period

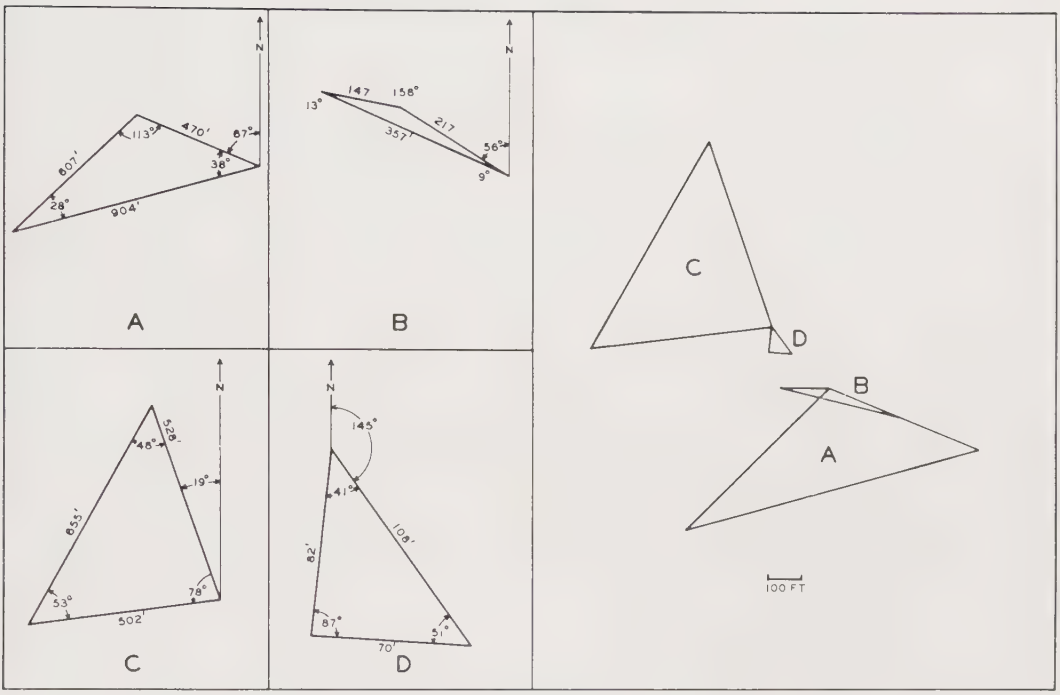

FIG. 1. Station orientations used in the collection of data. Instruments were located at the triangle apexes. Dimensions are given in the left half of the figure and relative positions and sizes are given in the right half.

and varied in total length from 12 hr to 2 weeks. Temperature was recorded simultaneously at three stations with relative positions according to Figure 1. Station locations are indicated by the apexes of triangles A, B, C, and D. The right half of Figure 1 is a scale drawing of the triangle orientation and spacing. The installations are located at the arrow point in Figure 5 (32°46′26.5″ N, 117°16′03.3″ W) which is 0.8 mile off the coast at San Diego, California in 60 ft of water.

Instruments were supported on aluminum poles fixed to cement tripods. The poles were expandable to 45 ft and were located at the apexes of triangles A and B. Five thermistors were fastened to each pole at regular intervals, and leads from the thermistors were laid on the bottom to a moored ship. With this arrangement, ship motion caused little strain on the leads, and there was no thermistor motion except through swaying of the poles with passing swell.

In addition, an LCM, a pontoon float, and an oceanographic tower were used as instrument platforms at the apexes of triangle C. The LCM and pontoon float were fixed with taut-line mooring to minimize horizontal movement.

The temperature measuring system used in triangles C and D consisted of three isotherm followers. The isotherm follower is an oceanographic instrument recently developed at the U.S. Navy Electronics Laboratory. It consists of an immersible transducer element, an electronic unit, an automatic winch, and two recorders. The winch is activated so that the transducer element seeks continuously the level of any prescribed isotherm. Depth (distance in feet below the surface) of the isotherm is recorded as a measure of the internal wave, and water temperature at the transducers is recorded for a visual check on the system. The isotherm to be followed is selected and changed at the operator's discretion. Alternatively, the transducer element may be stationed at any level and temperature fluctuations re-

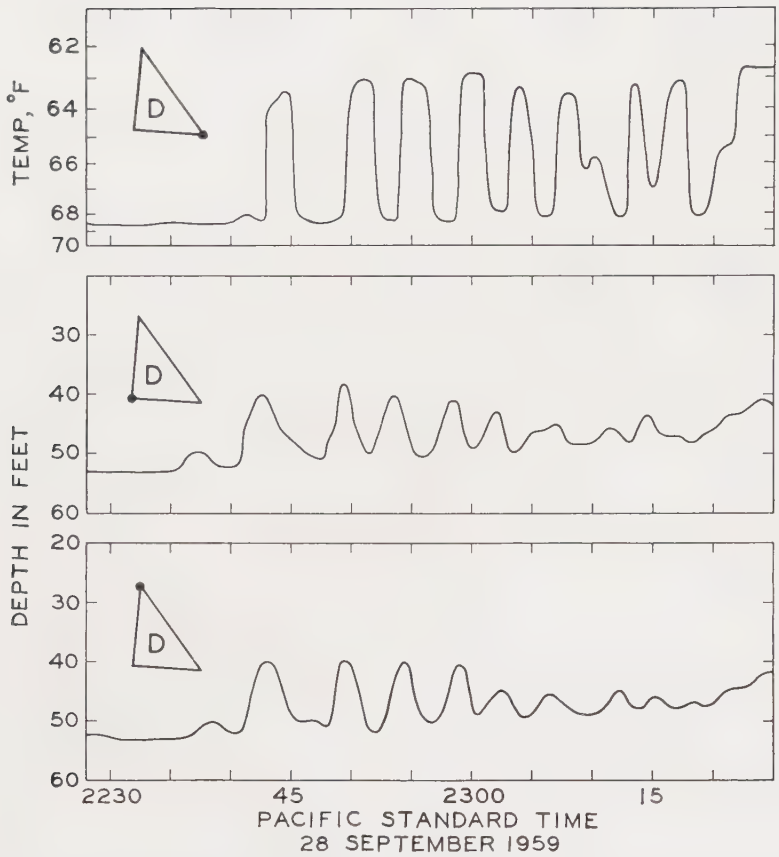

FIG. 2. Example of serial disturbances of the 67°F isotherm when the thermocline is near the bottom. The upper block represents temperature fluctuation at 50 ft (note the reversed ordinate) corresponding to isotherm displacement shown in the two lower blocks. The disturbances moved from left to right across the inset and the black dot shows where the trace in each block was recorded.

corded. Additional information on the instrument is given in LaFond (1961).

DESCRIPTION OF PHENOMENA

Thermal disturbances occurring in shallow water off San Diego were studied by discriminating between those that progress in series and those that progress individually. Figure 2 is an example of a series that was recorded in September, 1959, about 2 hr before low tide. The two lower traces represent the depth of the 67°F isotherm at locations indicated by the black dots on triangle D. The trace in the upper block represents temperature fluctuations caused by the same series of waves but recorded at the third apex of the triangle with the sensing element fixed at 50 ft below the surface. The abscissa in the upper block is inverted with respect to the usual orientation to present amplitudes of the temperature fluctuations in the upward direction. This presentation shows more clearly the relation between temperature changes at a fixed depth and corresponding changes in isotherm depth as shown in the two lower blocks. The average speed of this series was 20 ft/min shoreward within an angle of ±15° of the average direction of the series. The greatest speed of any wave relative to another was 6 ft/min.

Figure 3 is also an example of a serial disturbance measured at the three positions shown in the inset (triangle C), but in this case the thermocline was near the surface. The curves represent depth of the 64°F isotherm on 6 August 1959 about ¾ hr after high

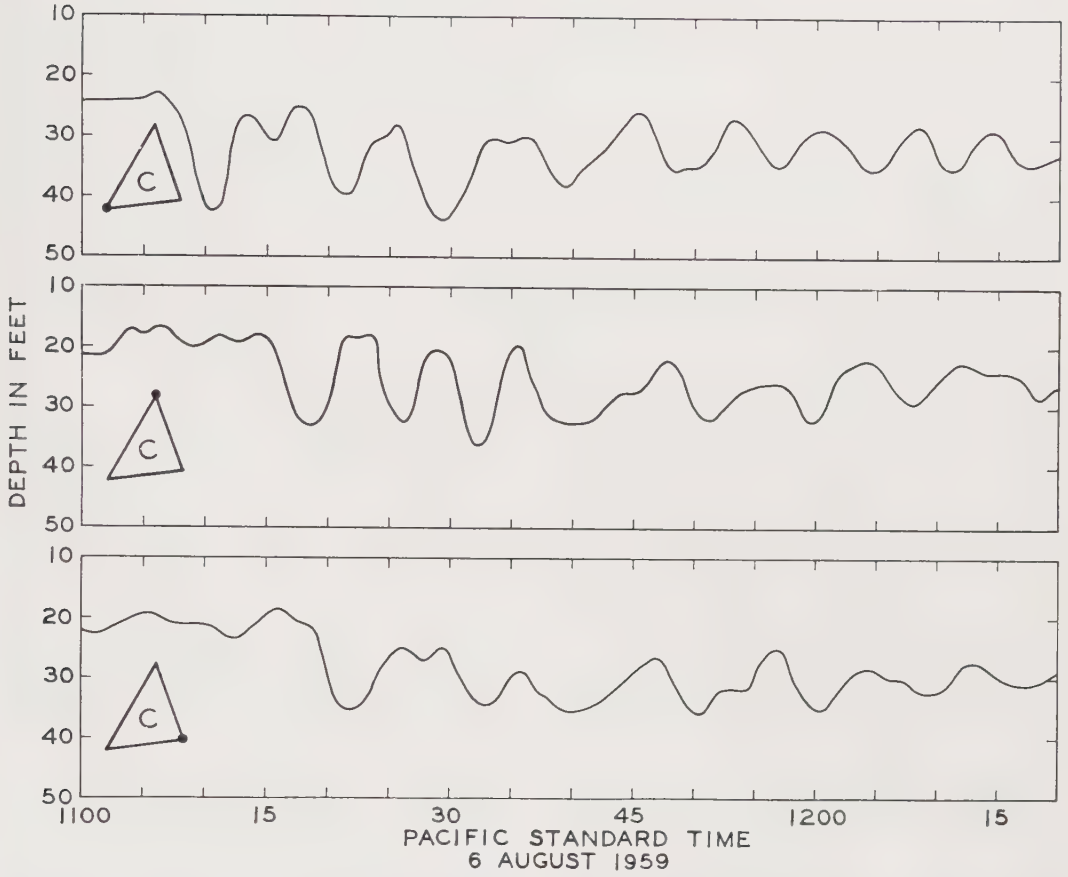

FIG. 3. Example of serial disturbances of the 64°F isotherm when the thermocline is located at about half the depth of the water. The disturbances moved from left to right across the triangle and the black dot indicates the place of observation.

tide. The waves were progressing about 40 ft/min toward shore within ±15° of the average. Maximum speed differential in this series was also 6 ft/min.

Internal waves more widely separated and not related to any particular tide phase progress in the same area. Figure 4 shows an example of a single wave that was measured at three stations in the relative positions indicated by triangle B. The time interval of the observations shown in the figure was approximately one hour which is about equal to the duration of a series of waves. The curves in each block are temperature fluctuations at fixed depths. Data at five depths are given in the two upper blocks, but only four depths are represented in the lower block owing to a short circuit in the thermistor at 11 ft above the bottom.

Some consistent features of internal waves observed in shallow water are well illustrated in Figures 2, 3, and 4. Continuous records over several tide cycles display serial waves when the thermocline is undergoing a low-frequency change. Data given in Figure 3 were taken when the thermocline was descending, and the thermocline was ascending when the series in Figure 2 were recorded. Close examination of the isotherms in Figures 2 and 3 with consideration for longer-period changes illustrates serial displacements in one direction with no compensating displacement on the opposite side of the equilibrium level. The same shape is

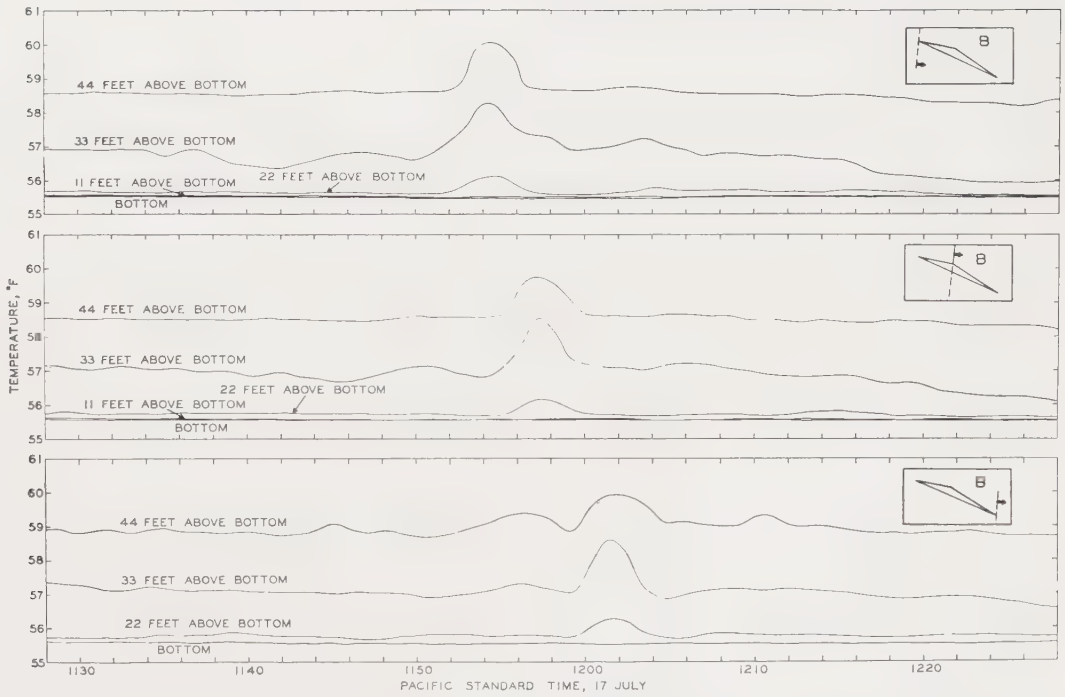

FIG. 4. Examples of a single internal wave measured at three stations at positions shown in the inset. The traces represent temperature fluctuation at fixed depths.

even more vividly displayed in waves that occurred singly. Displacement direction of these relatively high-frequency internal waves apparently depends only on the amplitude and the distance between the thermocline and bottom. When the average-thermocline level is at mid-depth or near the surface, the displacement is downward and when it is near the bottom the displacement is upward.

Relative velocities of the waves shown in Figures 2 and 3 indicate dispersion, and it follows that a series would not retain a fixed signature over space. A serial disturbance does exist until the waves are destroyed near shore, but the close spacing and high frequencies indicate an origin not far from the place of observation. These serial disturbances are interpreted as the result of one of two oceanic phenomena: 1) large-scale turbulence; turbulence has long been known to exist at the boundary between warm and cold water masses but probably not of the scale indicated by Figures 2 and 3 in such shallow water; 2) components of a larger internal wave that has dispersed into higher frequencies by breaking or some other process. Defant (1949) has published evidence that internal waves become unstable and possibly break upon approaching shallow water.

Temperature data collected in 1958–59 near San Diego were analyzed for resultant velocity of internal waves which have periods of approximately 5 to 15 min. Internal-wave velocities obtained from these data include the water current component which was not measured because the currents are weak and run generally perpendicular to the propagation direction of the internal waves. Measurements made at the bottom (60 ft) indicated that motion caused by swell is large compared to the current and that instantaneous measurements of current or even short period averages would have little meaning.

Certain assumptions were necessary before the data could be analyzed. The internal wave was assumed to travel at a constant speed with no acceleration or deceleration

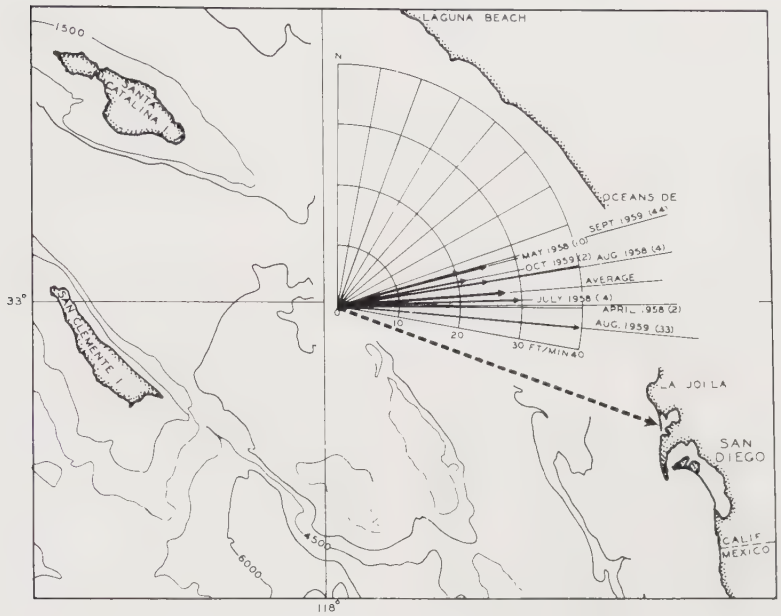

FIG. 5. Area off the San Diego coast where internal waves were observed. The inset summarizes data on the average speed and direction of internal waves at the place indicated by the arrow point. The numbers in parentheses, excluding August, 1958, are roughly proportional to the number of waves that occur in the corresponding month. Averages for each month are based on these numbers.

occurring in its travel across the three measuring stations. The direction of travel in all cases was assumed to be perpendicular to the crest line of the internal wave. Let the spans between any two of a trio of stations (such as those in Figure 1) be the a, b, and c legs of a triangle ξ and γ the angles opposite legs a and c respectively. From these considerations, the phase velocity V, is:

$$V = V_b \operatorname{Cos} \phi = V_a \operatorname{Cos} (\gamma - \phi) = V_c \operatorname{Cos} (\phi + \xi) \qquad (1)$$

where V_a, V_b, and V_c are phase-velocity components along the legs indicated by the subscripts.

From equation (1) it can be shown that the direction, ϕ, in which the wave is traveling relative to leg b is given by:

$$\phi = \tan^{-1}\left[\frac{V_b}{V_a} \operatorname{Csc} \gamma - \operatorname{Ctn} \gamma\right] = \tan^{-1}\left[\operatorname{Ctn} \xi - \frac{V_b}{V_c} \operatorname{Csc} \xi\right] = \tan^{-1}\left[\frac{V_c \operatorname{Cos} \xi - V_a \operatorname{Cos} \gamma}{V_a \operatorname{Sin} \gamma - V_c \operatorname{Sin} \xi}\right] \qquad (2)$$

The first equalities in equations (1) and (2) are identical to those given by Ufford (1947) which were derived from phase and wavelength considerations.

Computation of the velocity of internal waves by equations (1) and (2) is laborious, especially if data on a large number of internal waves are to be processed. The equations, in this form, suggest a graphical method of reducing the data which is much faster and equally accurate, since the accuracy in either case is limited to the accuracy at which one can determine phase of the same wave at three stations. The speed along any leg of the triangle can be considered a component of the internal-wave phase velocity, and if there is no acceleration the three vectors considered as points on a polar coordinate graph will describe a straight line which represents the crest or front of the wave. A line perpendicular to the crest line and passing through the origin will represent direction of progression, and its length between the origin and the crest will represent speed. Only two components are necessary to determine velocity of internal waves, and the third

component does not add to the accuracy since only two independent pieces of information can be obtained from observations at three stations.

In Figure 5 the average velocity vectors for various months and years at the same location are shown. The vectors are not entirely comparable because each one is based on different numbers of observations but, with the exception of August, 1958, the number of observations shown on each vector is roughly proportional to the number of waves that would occur in the indicated month.

An interesting point that emerges from the data given in Figure 5 is that the vectors representing the monthly averages are directed shoreward within an angle of only 30°. The spread of individual waves used to compute the averages is 90°. This particular quadrant is centered about the general shoreward direction. The narrow beam width of the average velocity vectors suggests that internal waves experience refraction, which is an opinion shared by almost all investigators of internal waves in shallow water.

Ufford (1947) and Ewing (1950) found internal waves in the San Diego area that travel in a general shoreward direction. Ufford (1947) gave the velocity vector of one wave that was directed offshore but this was in 3,750 ft of water. Ewing correlated sea surface slicks with internal waves and concluded that motion of internal waves drives the slicks over the sea surface. Time-lapse motion pictures by LaFond (1960) showed that band slicks moved shoreward with a general orientation parallel to shore. The internal waves represented in Figure 5 propagated in the same direction, and it is significant that none of the 109 individual waves moved in a direction away from or parallel to shore. Reflection of internal waves of periods from 5 to 15 min is therefore improbable unless the reflected waves are rapidly attenuated.

Ufford (1947) published values of internal-wave speed of progress ranging from 8 to 69 ft/min and Ewing quoted values of 31 and 43 ft/min. Vectors in Figure 5 suggest speeds somewhat higher in the summer months than wave speeds in the spring and fall, but this has not been consistently observed. Likewise, no consistent relation between direction of progress and season has been found. The average speed of all of the waves used to prepare Figure 5 is 27 ft/min in the direction of 5° north of east.

INTERNAL WAVES OF TIDAL PERIOD

Internal waves of tidal period have been recorded off the Southern California coast by Reid (1956) in 6,480 ft of water, by Emery (1960) in about 3,800 ft of water, and by Arthur (1954) at Scripps pier but in Arthur's case not consistently tidal. Emery reported an internal tide at a depth of about 200 ft near the northwest end of Santa Catalina Basin that lagged the Catalina Island surface tide by 2.5 hr. Reid found the internal tide between depths of 40 and 360 ft while anchored 40 nautical miles offshore. The results of his analysis showed the internal tide in phase with the surface tide at the coast. Emery noted that the highs and lows in Reid's internal-wave data lacked the asymmetry of the coastal surface tide.

The internal tide 0.8 mile off the San Diego coast was determined by averaging continuous records of isotherm depth, sampled at one-minute intervals, over one hour. These data are given as a smooth curve in Figure 6. Surface tide at the Scripps Institution of Oceanography is shown in the same figure. No fixed phase relation is evident in these data; instead, phase difference is clear and the difference in phase changes over the 7-day period regardless of how the surface tide is correlated with the internal tide. After considering a suggestion by Rudnick and Cochrane (1951) that internal tides originate at ocean boundaries, Arthur (1954) inferred from his thermograms from Scripps pier and Oceanside pier that there might not be a constant coupling between the surface tide and the internal tide phases in shallow water. These data are clearly in agreement with Arthur's suggestion. The two traces in Figure 6 are definitely out of phase near 1200 on the 22nd of September and almost perfectly in phase near 1200 on the 27th of September.

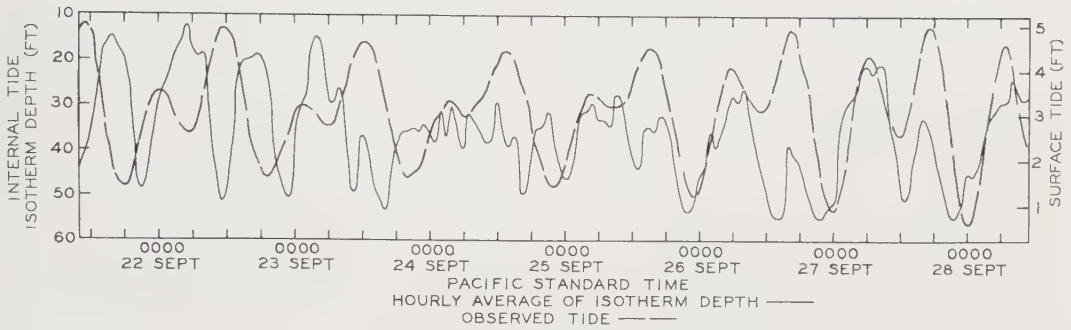

FIG. 6. Coastal surface tide and the internal tide measured 0.8 mile off the San Diego coast.

The autocorrelation and cross-correlation functions were evaluated using the surface tide and internal tide data, and the results are given in Figure 7. The autocorrelation curves show a small difference in periods of the two waves but the cross-correlation significantly shows that the surface and internal tides are best correlated at a period that is approximately equal to the surface tide. Evidently the slight difference in periods is real because the phase shift does not seem to be constant with respect to time.

If the surface tide and internal tide given in Figure 7 are approximated by two simple cosine functions, one phase lagged with respect to the other, it can be shown that at maximum and minimum values of $R_{1,2}(\tau)$:

$$\text{Tan}\,(w\tau + \phi) = -\frac{\text{Sin}^2\, w\zeta}{\zeta + \tfrac{1}{2}\,\text{Sin}\, 2w\zeta}$$

where $w = 2\pi/T$ and T is the period assumed equal here) of the two waves
τ = correlation lag
ζ = total length of each record
ϕ = a constant phase lag between the two waves

For sufficiently large ζ

$$\text{Tan}\,(w\tau + \phi) \cong 0$$

which is true when $\tau + (\phi/2\pi)T \cong (N/2)T$, where $N = 0, 1, 2. \ldots$ The last equation states that maximum and minimum $R(\tau)$ are displaced (from their location if there were no phase lag between the two waves) by an amount approximately equal to $(\phi/2\pi)T$ and that the interval of τ between maximum and minimum $R_{1,2}(\tau)$ is a measure of the period of the waves.

The most interesting point is that for $N = 0$ where $\tau \cong -(\phi/2\pi)T$. Thus, τ at the first maximum or minimum value of $R_{1,2}(\tau)$ is a measure of the average phase lag between the surface and internal tide. This particular value of τ in Figure 7 is about one hour which is similar to Emery's observation of lag between the Catalina surface tide and the internal tide in an offshore basin. This shallow-water observation of internal-tide period differs only slightly from Reid's observation in deep water but the asymmetry displayed in Figure 7 did not show in Reid's data. In this regard, Reid suggested that the internal tide originates in the action of the surface tide near the coast and that distortion takes place as it moves offshore. Analysis by Rattray (1957; 1960) also indicates significant changes in long internal waves as they propagate. Assuming the waves do originate near the coast, lack of consistent asymmetry in Reid's data might also be attributed to distortion.

For two days of the record, forces acting at higher frequencies influenced the average vertical movement of the isotherm. The origin of these higher-frequency fluctuations is unknown, unless instability of the form discussed in Defant (1949) occurred father offshore. However, the periodic forces that cause the internal tide can be accounted for by marking their average period in sequence through the interruption of the well-defined wave motion. Evidently the forces with 12-hr period persist through the interval of higher-frequency oscillations but are masked

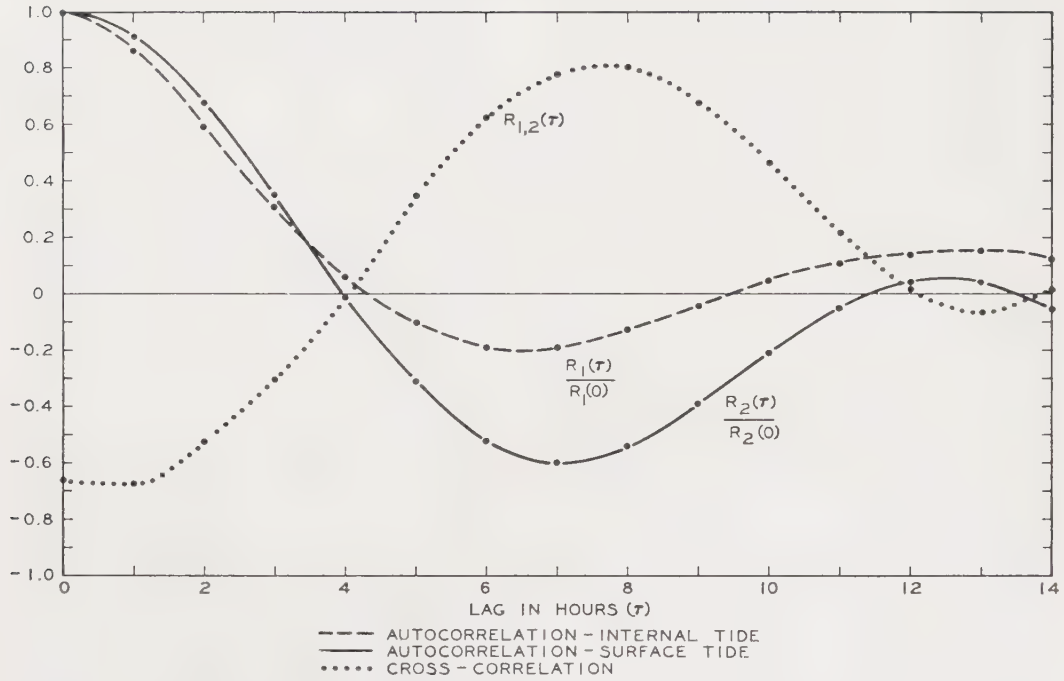

FIG. 7. Cross-correlation and autocorrelation of the surface tide and internal tide shown in Figure 6.

by other components of similar magnitude and dissimilar period.

Internal waves of tidal period found in these data have properties that are similar to the surface tide. Even when the internal tide is not apparent in the record, forces with a 12-hr period seem to be acting as indicated by Figure 6 and the correlation curves in Figure 7. The word "forces" is used in the sense of balance of pressure and gravity forces. The data in general seem to support Reid's theory that these waves are free and result from tide action near the coast. The phases of the two phenomena are not consistently coupled and this is not fully understood. The fact that vertical gradients exist in tide-current velocity in shallow water is an indication of phase shift between the surface and internal tides. Reid's data on internal tides in deep water and the profiles of internal waves in Figures 2, 3, 4, and 6 suggest that differential response of the two phenomena to boundary conditions is the explanation for the inconsistent phase relation in shallow water.

SUMMARY AND CONCLUSIONS

Relatively large amplitude internal waves with relatively short periods are identifiable without the aid of spectrum analysis over distances up to 1,000 ft in shallow water. These waves (see above) have been observed in 60 ft of water, 0.8 mile offshore, in trains of several waves and as waves essentially isolated from any other similar disturbance.

Isotherm displacement, associated with wave periods from 5 to 15 min, is analogous to surface waves propagating in very shallow water. The displacement is downward with no compensating displacement on the opposite side of the undisturbed level unless the thermocline is near the bottom and in this case the displacement is upward.

The average velocity of internal waves with periods from about 5 to 15 min is 27 ft/min in a direction which is essentially perpendicular to the shore line at San Diego, California. Variation in the speed and direction is not clearly related to season. The data indicated that internal waves refract but no

evidence that internal waves reflect was found.

Internal-wave components of tidal frequency persist throughout the 7 days of observation although they are obscured for about 2 days. Asymmetry in the internal tide is similar to the surface tide but the two phenomena are not constantly in-phase nor is there a consistent phase-shift. The variable phase relation is attributed to different effects of boundary conditions on the two phenomena.

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A NOTE ON STABILITY IN CENTRAL FLORIDA LAKES, WITH DISCUSSION OF THE EFFECT OF HURRICANES[1]

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ABSTRACT

Limnological data are presented that indicate that central Florida lakes in summer normally do not overturn at night even though night temperatures are lower than that of the bottom water during the day. This is attributed to the usual lack of wind at night. Wind and rain effects on these shallow lakes are shown before and after tropical storm "Brenda" and hurricane "Donna." It is concluded that the relatively mild Brenda was as effective in initiating overturn as was the much stronger Donna.

INTRODUCTION

Studies are in progress on lakes in the vicinity of Winter Haven, Florida, in connection with production of chironomids. Information of general limnological interest was obtained on the stability of these subtropical lakes. In addition, data were acquired before and after tropical storm "Brenda" and hurricane "Donna" showing some of their effects on these lakes.

The help of the following persons is much appreciated: H. J. Hutton, F. D. Seibert, and F. B. Thompson, Jr. I wish to thank Dr. D. G. Frey for criticism of this paper and for providing useful references.

STABILIZING INFLUENCES IN SUMMER

Diurnal limnological studies on shallow tropical and subtropical lakes are few, but Ruttner (1931) and Beadle (1932) studied large and relatively deep tropical lakes, and Singh (1955) and Vaas and Sachlan (1955) studied diurnal variation in shallow tropical waters. Ruttner showed that the temperature of Ranu Lamongan from the surface to 5 m was lower throughout at 0515 hr than the temperature at 5 m at 1430. His data indicate that there was not a strong diurnal chemical stability within the upper 5 m in this deep lake. Beadle's data also show a lack of chemical stability, in Lake Naivasha, during the period from 0600 to 1230, due probably to the strong winds characteristic of the region. Thus, these large and relatively deep lakes apparently circulate daily in the upper zone.

The shallow inland waters of India, according to Singh (1955), have a daily circulation also, resulting from "strong winds, extreme temperatures and convection currents." After a calm night, however, ponds may be covered with dead fish and have low oxygen concentrations, implying a lack of circulation. Vaas and Sachlan (1955) studied a fishpond 60 cm deep and a small pit 2 m deep. The pit was without wind action but showed mixing of chemical factors to a small degree. The much larger but very shallow fishpond circulated freely diurnally, presumably due to wind effects and convection currents.

As can be seen in Figure 1, Lake Cannon and Lake Deer, in central Florida, do not overturn in summer except under special conditions. The temperature of the entire lake at night is at or below that of the bottom during the day. One would expect this to result in a complete overturn of the lake at night; the dissolved oxygen data, however, indicate that the lakes do not usually overturn at night, but rather remain stable. The maximum and minimum air temperatures for the period represented in the figures for Lake Cannon were 33.9 and 22.2°C; those for Lake Deer were 33.3 and 22.2°C. Thus, convectional cooling by itself is not adequate to disrupt the chemical stratification. This was true of every diurnal series we have made, except when there was considerable rainfall or night winds. The situation may be

[1] Contribution No. 103, Florida State Board of Health, Entomological Research Center, Vero Beach. This investigation was supported by Public Health Service Grant RG-7587, from the Division of General Medical Sciences.

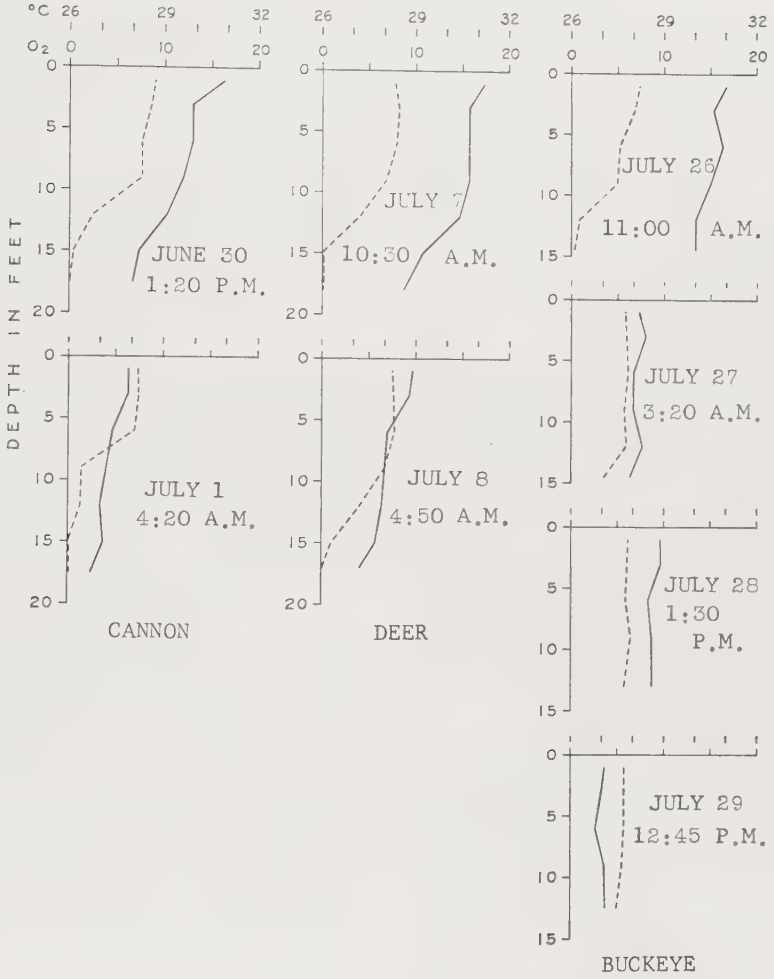

FIG. 1. Distribution of temperature (——) and oxygen (– – –) in Winter Haven lakes during normal weather and during tropical storm "Brenda."

summarized as follows. Normally, winds occur only during the daytime, chiefly in the afternoon. At this time, the lake is stable thermally with high temperatures at the surface. Although at night there is enough heat loss to permit overturn, turbulence resulting from nocturnal cooling alone does not disrupt the chemical stratification; rainfall or wind appear to be necessary to cause overturn. To contrast with this normal occurrence, the effect of rainfall and night wind is illustrated from Lake Buckeye, showing not only heat loss, but also overturn occurring at night as a result of the influence of tropical storm Brenda discussed below.

TROPICAL STORM INFLUENCES

The center of tropical storm Brenda did not come to the Winter Haven area, but its effect was felt in the form of moderate winds on July 27 and 28 and heavy rainfall on July 28 and 29, 1960. According to the City Fire Department, 2.78 in. of rain fell from 0730 on July 28 to 0730 on July 29. The last vertical series was taken at 1245 on July 29, at which time and during the morning, heavy rains were still coming down. We probably had therefore from 3.5 to 4 in. of rain before the series, with steady winds of 7 mph and gusts up to 22 mph, according to the Bartow Air Base, located near Winter Haven.

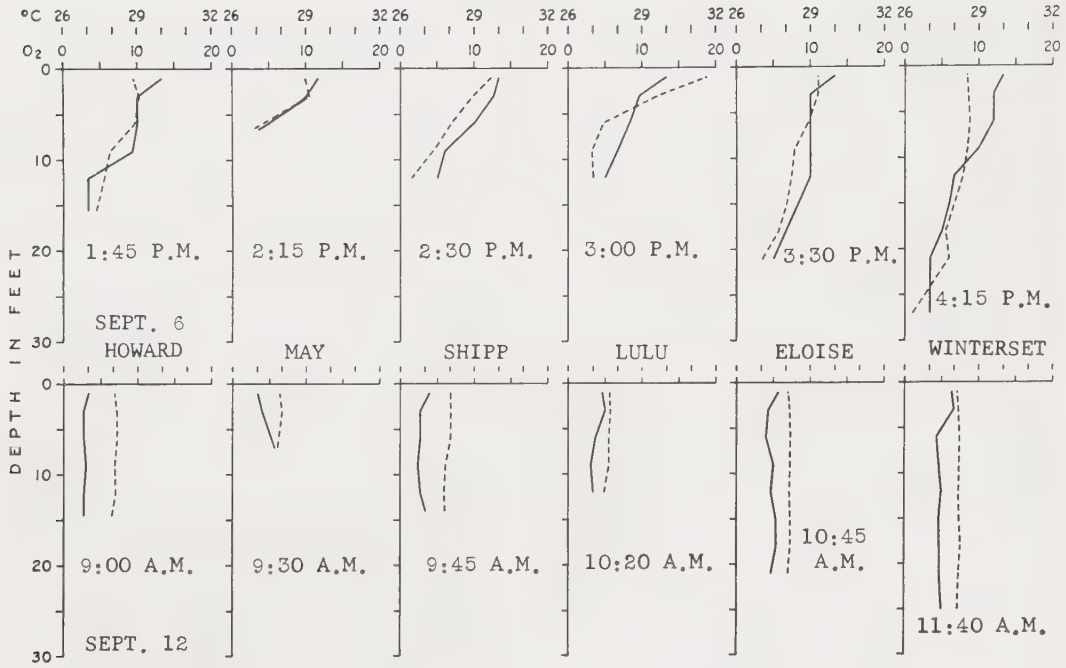

FIG. 2. Distribution of temperature (——) and oxygen (– – –) in Winter Haven lakes before and after hurricane "Donna."

Vertical series of samples were taken on Lake Buckeye (Fig. 1), an isolated lake with no inflow or outflow, before and during the storm. It is evident from the figure that overturn was complete as a result of the storm's influences. The first series taken before the storm shows that the whole lake was warm, with the major oxygen reduction occurring between 9 and 12 ft. The second series taken during the beginning of the storm shows considerable cooling from night winds, with the major oxygen reduction between 12 and 15 ft. The third series taken at the height of the storm shows that the lake had warmed up over the night series before, but was considerably cooler than during the day series of July 26; the oxygen picture reveals a complete breakdown of stratification from both wind and rain effects. Finally, the last series taken at the end of the storm shows that the lake had continued to cool, being considerably cooler even than the earlier night series, with oxygen showing that stratification was still disrupted. Wind and rain thus were the chief factors involved in the disruption of stratification.

The center of hurricane Donna passed directly over Winter Haven just before midnight September 10, 1960, accompanied by heavy rains. The rain gauge at the City Fire Department blew away, but the nearby Citrus Experiment Station reported 8.10 in. and 1.40 in. on September 10 and 11, respectively. Maximum wind intensity for the area, measured by the U. S. Weather Bureau in nearby Lakeland, was 90 mph in gusts, with a steady measure of 68 mph.

A vertical series of samples was taken in the center of six lakes connected by a series of shallow canals, all of which drain into the Peace River over a small dam that is open only during unusually high-water periods. Temperature and dissolved oxygen were measured both before and after the hurricane (Fig. 2). Overturn was complete, each lake being homogeneous in regard to these factors. Incidentally, lawn mowings and spanish moss were recovered from the bottom of Lake Winterset and Lake Eloise on the anchor of the boat; they were still bright green as if wet by a normal rain. The unusually high oxygen values near the surface in

Lake Lulu and Lake Shipp before the hurricane can be explained—these lakes have a much higher algal count in the surface waters than the others, and are consequently supersaturated. The apparent reason is that these lakes receive greater quantities of nutrients than the others, Lake Lulu receiving the city sewage and Lake Shipp receiving wastes from citrus and vegetable canning plants and a fertilizer plant.

DISCUSSION

It is apparent that in these central Florida lakes, stratification in summer normally is not disrupted by turbulence resulting from nocturnal cooling alone; moderate wind during the afternoon also does not disrupt stratification. Rainfall and nocturnal wind, however, do result in overturn, as during tropical storm Brenda. Overturn resulting from Brenda's relatively small influence on the area was as complete as overturn resulting from the great influence of hurricane Donna, whose "eye" passed directly over the area. In deep lakes, however, the relative effects of heavy rainfall alone and heavy rainfall with hurricane winds may be considerably different from those reported here, for Hutchinson (1957 p. 451–2) showed that temperature was hardly changed below 10 m in Linsley Pond, Connecticut, during the hurricane of September 21, 1938, and Kufferath found that rainfall may "induce local mixing well into the otherwise stagnant water below the thermocline" in the (deep) Lake Tanganyika (Hutchinson 1957 p. 462).

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SUMMER TEMPERATURES IN LAKE SCHRADER, ALASKA[1]

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ABSTRACT

Lake Schrader is a deep arctic lake on the northern slope of the Brooks Range, Alaska, at a latitude of 69°N. Field investigations covered two summers, the warm summer of 1958 when the ice cover lasted until June 28, and the cool summer of 1959 when the ice left the lake on July 26. Thermal studies revealed that the lake developed and maintained a stable stratification between 4.5 and 10.5°C in 1958 but did not reach 4°C by mid-August, 1959.

INTRODUCTION

Thermal studies of arctic lakes have been carried out mostly on shallow lakes, such as those of the northern slope of Alaska. Brewer (1958) found no summer stratification in these lakes, and Livingstone, *et al.* (1958) confirmed this for a slightly deeper series of lakes in the same area. The latter investigators also examined Chandler Lake in the Brooks Range and on August 15, 1951, recorded a temperature gradient of less than one degree in 18 m (maximum depth 21 m).

When a permanent camp was set up in the Brooks Range at Lake Peters, the author was able to investigate Lake Peters and nearby Lake Schrader, two deep glacial lakes. Thermal studies in Schrader showed that a great variation may occur from year to year, as there was a well-developed stratification in 1958 but none in 1959.

Lake Schrader lies at the northern edge of the mountain front along the boundary of the foothills (Payne, *et al.* 1951). Low hills bound the lake on three sides, while Mt. Chamberlin and the flat land separating the two lakes make up the fourth. Although the hills give the lake some wind protection, a relatively strong wind (valley breeze) blows along the lake during the day (de Percin 1958). In 1958 this wind averaged between 18 and 27 km/hr.

Lake Peters lies immediately upstream from Lake Schrader. Thus, although there are at least 6 small glaciers in the drainage basin of the latter, most of the melt water enters Lake Peters, and much of the glacial material settles out before the water reaches Schrader. The milky Peters effluent may still be traced for almost 1 km after it enters Schrader, however, and the glacial turbidity does cut down the transparency of the water. As a result, the Secchi disc reading was only 3 to 4 m in 1958, much less than might otherwise be expected in such an oligotrophic lake (Hobbie 1960).

At this latitude (69° N) the summers are short and cool, winters long and cold. Barter Island weather station, 100 km to the north, has a 4-year average temperature of –12.8°C and a July and August average of around 4°C (U. S. Weather Bureau Climatological Records from Alaska). The ice remained on the lake until June 28 in 1958, and until July 26 in 1959.

The lake is fairly narrow with only one basin (Fig. 1). A large alluvial fan on the southeast side is the sole break in the otherwise regular shore line. Morphometric data are given in Table 1.

METHODS

Temperatures were taken with a thermistor probe used with two different recorders, a Leeds and Northrup Wheatstone Bridge in 1958 and a modified Varian continuous trace recorder in 1959. Readings in 1958 (Station 2) were made at 1.5-m intervals for the top 7.5 m and then every 3 m thereafter. All 1959 readings, taken in the deepest part of the lake, were at 3-m intervals. Air temperatures were measured in a standard U. S. Weather Bureau shelter and winds with a Bendix-

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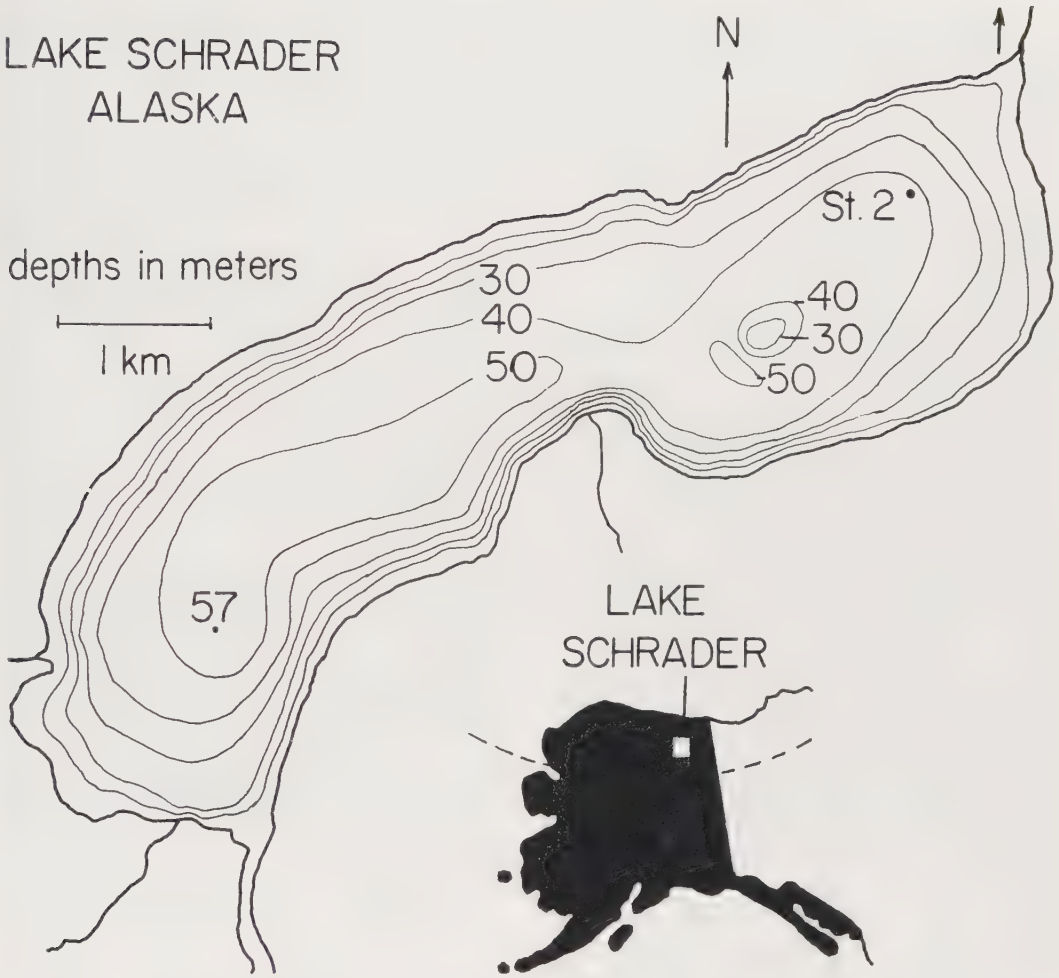

FIG. 1. Location and bathymetric map of Lake Schrader, Alaska.

Friez totalizing anemometer, both at the Lake Peters camp. More than 300 depths were measured with a steel tape along 10 sounding runs for construction of the bathymetric map shown in Figure 1.

RESULTS

Measurements in the middle of August show that the lake was stably stratified at this time (Fig. 2). Oxygen measurements covering a longer period of time indicated that the stratification was present at least by July 31 (Hobbie 1960). Judging from the low hypolimnetic temperature, complete circulation stopped soon after the ice left the lake.

In 1959 the ice lasted until July 26, 4 weeks longer than the previous year. By this time the amount of daily radiation had decreased greatly from the June peak, and the rate of heat uptake by the water was low. As seen in Figure 3, the lake not only failed to stratify, but had not even reached a temperature of 4°C by August 14.

TABLE 1. *Morphometric data for Lake Schrader, Alaska*

Area	(km^2)	13.2
Greatest length	(km)	8.1
Greatest width	(km)	2.4
Mean width	(km)	1.6
Maximum depth	(m)	57
Mean depth	(m)	33
Altitude	(m)	852

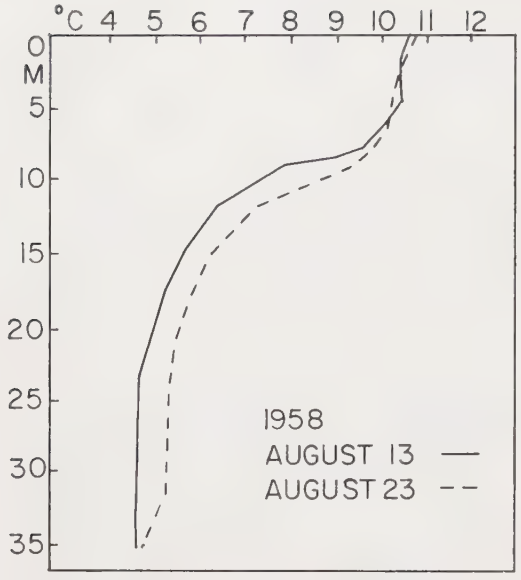

FIG. 2. August, 1958, temperatures at Station 2, Lake Schrader.

Although 1959 was slightly windier than 1958 at the Lake Peters station, the difference was small. From July 11 to August 27, 1958, the total wind movement averaged 127 km/day, while in the period July 1 to August 13, 1959, the average was 150 km/day. Simultaneous records of wind movement at Peters and at Schrader from August 3–11, 1959, showed that Schrader was windier, having a value 1½ times that of Peters.

A much greater difference between the two summers is noticeable when the thawing degree-days are compared (Table 2). Thawing degree-days are the average daily temperatures in excess of 32°F (Linell 1953).

Two important contrasts are seen in Table 2, one between Peters and the two coastal stations, and the other between the two summers. The Peters area had higher temperatures than the coastal regions at all times because of its inland location. When the two summers are compared, 1958 was obviously warmer than 1959. In fact, de Percin (1958) states that 1958 was far warmer than average at Barter Island.

The air temperatures are influenced, of course, by cloud cover and air movement, and all three factors affect the duration of the ice sheet. During cool summers the open water arrives so late that rapid heating does not occur. This slow uptake of heat, along with the stormy weather that often accompanies cool summers in this region, precludes any thermal stratification. In the event of a very warm summer, the ice melts relatively early, and high rates of heat uptake during the long hours of daylight allow stratification.

It is impossible to say that these two

TABLE 2. *Degree days (above 32°F) during the summers of 1958 and 1959 at three stations in arctic Alaska*

Station	April	May	June	July	August	Total	Total 12 July to 27 August
				1958			
Barrow	3	0	88	186	330	607	417
Barter	7	3	145	434	395	984	647
Peters				398*	453*		851
				1959			
Barrow	0	1	120	138	166	425	211
Barter	0	1	51	219	120	391	203
Peters		9	291	302	271**	873**	466

* 1958 records from 12 July to 27 August
** 1959 records from 29 April to 27 August

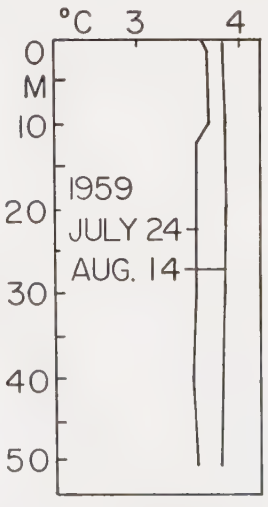

FIG. 3. July and August, 1959, temperatures at the deepest point of Lake Schrader.

examples are the extremes of thermal conditions for this lake. However, these data, plus the data on other lakes previously mentioned, lead me to postulate that in an "average" summer, the lake does not stratify permanently but only temporarily if at all. Temperatures within the lake might be between 7° and 9°C.

Hutchinson (1957) has pointed out the inadvisability of using geographic terms to describe the thermal characteristics of lakes. Lake Schrader is a good example of how these terms can be misleading, for under the Forel-Whipple system (Whipple 1927) it would be classed as 2nd order temperate one summer and 2nd order polar the next. According to the recent system of Hutchinson and Löffler (1956), the lake was dimictic in 1958 and monomictic in 1959. According to their diagram relating altitude and latitude to expected classification types, Schrader should be a cold monomictic lake. The variability of the thermal regime indicates that the lake is close to the northernmost limit for dimictic lakes. Indeed, this is the farthest north a dimictic lake has yet been recorded in western North America.

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THE LIMNOLOGY OF CANYON FERRY RESERVOIR IV. THE ESTIMATION OF PRIMARY PRODUCTION FROM PHYSICAL LIMNOLOGICAL DATA[1]

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ABSTRACT

Biological rates of oxygen production and consumption were computed by adding the rates of turbulent transport of oxygen to the observed rates of change in concentration at successive depths. This involved using coefficients of vertical eddy diffusivity which were assumed to be equivalent to coefficients of vertical eddy conductivity, computed on the basis of a heat transport equation utilizing Birgean heat budgets. An attempt was made to assess the validity of the coefficients as follows. In the clinolimnion, the average values of the coefficients were similar when computed either on the basis of temperature change with depth and time or on the basis of the heat transport equation. A satisfactory correlation was obtained between the coefficients and a function of shearing stress (velocity gradient) and resistance to mixing (stability). The coefficients decreased with increasing depth in the epilimnion, became minimal and constant in the metalimnion and increased in the hypolimnion. Oxygen consumption exceeded oxygen production below 5.5 m and was maximal just below the euphotic zone (9–12 m). Oxygen consumption was minimal in the metalimnion and increased in the hypolimnion. An oxygen concentration maximum was correlated with the metalimnetic oxygen consumption minimum. Euphotic zone oxygen production equivalent to dysphotic zone oxygen consumption amounted to 1.01 g O_2/m^2/day. Euphotic zone respiration would have been 1.21 g O_2/m^2/day if it proceeded at the same rate as in the 9- to 12-m stratum. On the basis of the ratios, oxygen consumption/chlorophyll and oxygen consumption/seston euphotic zone respiration amounted to 1.44 g O_2/m^2/day and 2.01 g O_2/m^2/day respectively. Gross production values then would range between 2.22 g O_2/m^2/day and 3.02 g O_2/m^2/day. The latter value was extremely close to black and clear bottle estimates of 3.00 g O_2/m^2/day.

INTRODUCTION

In previous papers (Wright 1958, 1959, 1960) estimates were made of gross and net primary production in Canyon Ferry Reservoir by means of oxygen changes in black and clear bottles. This paper is concerned with an attempt to estimate primary production from physical data collected during the summer of 1958.

Hutchinson (1938) has shown that in holomictic lakes between 20 and 75 m deep the relative areal hypolimnetic oxygen deficit between vernal circulation and the height of summer stagnation appears to give a fair indication of the biological productivity of the lake. More recently, Ohle (1956) discussed the relationship between hypolimnetic metabolism and lake productivity.

In a more rigorous treatment, Hutchinson (1957) corrected the mean rate of uptake of oxygen in hypolimnetic water of Lake Mendota by addition of the rate of passage of oxygen into the hypolimnion as a result of vertical eddy diffusion. Assuming that the over-all rate of oxidative metabolism in Lake Mendota was about the same at all depths, a total rate of net production of 0.118 mg O_2/cm^2/day was computed.

The determination of reliable average coefficients of vertical eddy conductivity which are considered to be equivalent to coefficients of vertical eddy diffusivity is the most difficult part of the procedure. Schmidt (1925) and Mortimer (1941–1942) used the heat transport equation

$$\frac{\delta H}{\delta t} = A_z \frac{\delta T}{\delta Z} \qquad (1)$$

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and simply computed the rate of increase in the heat content of a column of water below a certain depth over a designated period ($\delta H/\delta t$) and divided this by the value of the mean thermal gradient at the depth under consideration ($\delta T/\delta Z$). Hutchinson (1957) has pointed out that calculations of $[H]$ are heat budgets computed for unit areas of planes at various depths by the method employed by Forel. This method of computing heat budgets appears to be invalid, as it gives impossibly high results for summer heat income when applied to certain lakes. The correct procedure would be to determine the rate of increase in heat for the entire body of water in question and then express this per unit area of the plane (Birgean heat budget). The latter procedure is applicable only to any plane above the depths at which lateral heating is significant.

Hutchinson (1941, 1957) also determined eddy conductivity coefficients which were derived from temperature changes following the procedure of McEwen (1929). It can be shown that if A_z is constant over a given range of depths, then the second order equation (2) holds where θ is temperature, z is depth, and t is time.

$$A_z = \frac{\delta\theta}{\delta t} \Big/ \frac{\delta^2\theta}{\delta z^2} \qquad (2)$$

McEwen pointed out that in general the temperature curve in the thermocline and the upper part of the hypolimnion of a thermally stratified lake can be fitted to an expression of the form

$$(\theta_z - C) = C_1 e^{-az} \qquad (3)$$

where C_1, C, and a are constants to be determined empirically. Whenever the temperature curve can be legitimately expressed by equation (3) and when A_z is also constant then the following holds:

$$\frac{\delta\theta}{\delta t} = Aa^2 C_1 e^{-az} \qquad (4)$$

$$= Aa^2(\theta_z - C)$$

Full directions are given in Hutchinson (1941).

With Linsley Pond data, a constant value of A_z was found in the thermocline and upper hypolimnion (clinolimnion) when McEwen's procedure was used. The heat transport equation gave similar results when the rates of heat increase were computed on a Birgean basis. However when computed on a Forelian basis the values of A_z exhibited a steady rise with depth. On the basis of Munk and Anderson's (1948) treatment, Hutchinson (1957) has pointed out that only if there is a constant distribution of horizontal velocities will A_z increase as stability decreases with depth in the hypolimnion. The data resulting from the use of McEwen's (1929) procedure can be explained if the rate of decline of velocity with depth in the clinolimnion is proportional to the square root of stability. Below the clinolimnion, McEwen's treatment cannot be used and Hutchinson concluded that there was no way of ascertaining what values of A_z apply in the hypolimnion.

METHODS

Temperature data were obtained with a bathythermograph. A total of 12 temperature series was obtained during May 30 and August 27, 1958, from the lower end of the reservoir. Eight of the series were averages of temperatures taken from 9 different stations; 3 were averages from 8 stations; and one was an average from 3 stations. It was felt that in averaging temperatures from many stations the effects of water movements in altering temperature distribution would be evened out. In addition to these series which were used as the basis for computation of A_z, an additional series was taken in June when 6 additional stations were occupied on 4 cruises. The results of these, in addition to data from the other 9 stations, were used for estimating current velocity by the dynamic height method.

Seven series of oxygen determinations taken between June 7 and August 27 were available for computation of oxygen consumption. For each series, depths were sampled from the surface to 150 ft at 10-ft intervals at a central station in the lower end of the lake.

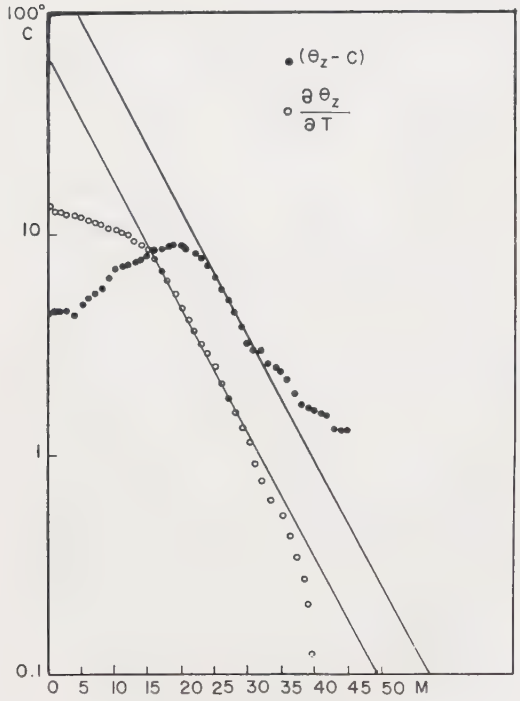

FIG. 1. Semilogarithmic plots of $(\theta_z - C)$ and of $\delta\theta/\delta t$ against Z, for the mean temperatures and temperature changes from May 30 to August 27, 1958. $C = 6.36°C$.

VERTICAL EDDY CONDUCTIVITY

McEwen's method was applied to calculate coefficients of vertical eddy conductivity in the clinolimnion. In Figure 1, semilogarithmic plots of $(\theta_z - C)$ and $\delta\theta_z/\delta t$ against z are given using mean values of θ for the period from May 30 to August 27, 1958. The plot of $(\theta_z - C)$ shows that, in the region between 24 and 31 m, equation (3) may be used. The rate of heating expressed by equation (4) falls exponentially and parallel to $(\theta_z - C)$ in the region between 24 and 31 m. In this zone the assumption of a constant value of A_z is therefore valid.

Values of A_z computed by the use of equation (4) are given in Table 1. These values are compared with coefficients computed using equation (1) when $\delta H/\delta t$ was computed on both a Forelian and a Birgean basis. The variation in the individual values of A_z for each depth is regarded as the result of statistical error. When mean values are compared, it is evident that the same result is obtained from the use of equation (4) or equation (1) when the rate of heat increase in the latter is computed on a Birgean basis. When used with Forelian heat budgets, equation (1) yields values of A_z which are very much in excess of those computed by the other two methods, thus confirming Hutchinson's (1957) results with Lake Mendota and Linsley Pond data.

The second order equation (2) cannot be used in the epilimnion and hypolimnion, hence resort must be made to the first order equation (1) for calculation of A_z. As Hutchinson (1957) has pointed out, heat can enter the hypolimnion by mechanisms other than vertical turbulent transport. In small lakes, such as Linsley Pond, profile-bound density currents may transfer heat in the hypolimnion. Although such currents would not appear to be important in large lakes, the

TABLE 1. *Analysis of thermal conditions in the clinolimnion of Canyon Ferry Reservoir, May 30–August 27, 1958*

Z (m)	θ (°C)	$\delta\theta/\delta t$ (°C/month)	A_z (g/cm/sec)		
			Equation (4)	Equation (1)	
				Birgean basis	Forelian basis
24	9.33	2.42	0.111	0.149	0.216
25	8.85	2.15	0.118	0.109	0.160
26	8.50	1.91	0.129	0.122	0.181
27	8.18	1.69	0.136	0.115	0.176
28	7.90	1.47	0.129	0.125	0.197
29	7.70	1.26	0.139	0.134	0.211
30	7.49	1.08	0.134	0.112	0.181
31	7.28	0.96	0.142	0.124	0.215
Average			0.129	0.124	0.192

possibility of heat exchange with the portion of the bottom which is alternately in contact with the epilimnion and hypolimnion as a result of internal seiches cannot be neglected. Dutton and Bryson (1959) have found that this latter mechanism can account for a significant portion of the heat transport through the thermocline.

On the basis of Munk and Anderson's (1948) theory of formation of the thermocline, coefficients of vertical eddy conductivity should be proportional to a function of the current velocity gradient and the square root of the stability gradient. Riley (1951) obtained a reasonably accurate empirical proportionality between "observed" coefficients of vertical eddy diffusivity and conductivity and a function of the mean current speed and stability in sea water. On the basis of these considerations, more confidence could be placed in the computations of A_z if a reasonable relationship could be demonstrated between A_z and the factor generating turbulence (shearing stress) and the resistance to turbulent mixing (stability).

Current velocities were computed by the dynamic height method, as modified for lakes by Ayers (1956) and Ayers and Bachmann (1957). The calculations were based on a series of 4 synoptic cruises taken in June, 1958, during which bathythermograph records were obtained from 15 stations in the lower end of the lake. Differences in dynamic heights were calculated between pairs of stations for each cruise. Average current between stations at 5-m depth intervals was computed on the basis of the average of the slopes of the dynamic surfaces for the 4 cruises. The average of the current speeds of all stations at 5-m intervals was then determined. From these data, the average velocity gradients were computed. Stability values were computed from the density gradient of water between the depth in question and the depth one meter below. The ratio of the velocity gradient to the square root of stability for several depths is compared with values of A_z computed from June heat budget data in Table 2.

In Figure 2, coefficients of vertical eddy conductivity are plotted against the corresponding function of velocity gradient and the stability. A reasonably good fit is apparent between the two variables. Since the thermocline is at shallow depths in June, the graph portrays the relationship between values of A_z and the associated velocity and stability functions in both the epilimnion and hypolimnion. The relationship is consistent enough to lead one to suspect that most of the heat which enters the hypolimnion is transported by turbulence and that other mechanisms of hypolimnial heating are insignificant. It is apparent, also, that in water of slight stability such as occurs in the hypolimnion small velocity gradients will result in appreciable coefficients of vertical eddy conductivity. It is not surprising that higher values of A_z appear in the hypolimnion than in the thermocline where shearing stress could be expected to be greater but counteracted by increased stability. Lathbury, Bryson, and Lettau (1960) have demonstrated that not only may currents be induced in the hypolimnion by internal seiches but that there are quasi-steady currents in the hypolimnion which are not due

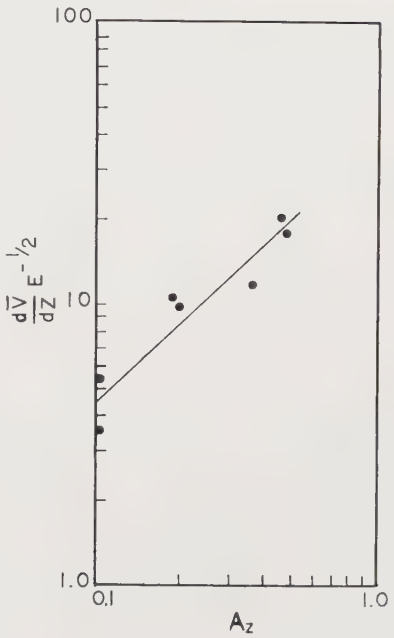

FIG. 2. Log-log plot of coefficients of vertical eddy conductivity plotted against a function of the mean velocity gradient and the stability.

TABLE 2. *Coefficients of vertical eddy conductivity compared with a function of velocity gradient and stability, June, 1958*

Depth (m)	E (g/cm²/cm×10⁻⁵)	$E^{1/2}$ (g/cm²/cm×10⁻⁴)	$\bar{V}$ (cm/sec)	$\frac{d\bar{V}}{dZ}$ (cm/sec/cm×10⁻²)	$\frac{d\bar{V}}{dZ}E^{-1/2}$	A_z (g/cm/sec)
S	25.1	5.01	4.40	0.90	18.0	0.47
5	67.1	8.19	3.50	1.66	20.3	0.46
10	65.4	8.09	1.84	0.96	11.9	0.36
15	44.8	6.69	0.88	0.37	5.5	0.10
20	19.7	4.44	0.51	0.16	3.6	0.10
25	5.4	2.32	0.67	0.23	9.9	0.20
30	4.6	2.14	0.44	0.23	10.7	0.18
35	1.4	1.18	0.21			0.26

to internal seiches and which are of appreciable magnitude.

Coefficients of average vertical eddy conductivity for the period May 30 to August 27 were computed at all depths by the use of equation (1). The rate of heat increase was computed on a Birgean basis. The average values for 3-m depth intervals are presented in Table 3.

OXYGEN CONSUMPTION

The rate of change of a non-conservative property such as oxygen concentration is a function of the biological rate of change and the physical rate of change brought about by diffusion and advection. In the following discussion, advection has been ignored and equation (5) was applied where $\delta O_2/\delta t$ is the observed rate of change in oxygen concentration below a unit plane surface, A_z the coefficient of vertical eddy diffusivity, $\delta O_2/\delta z$ the average vertical gradient of oxygen concentration across the plane surface in question and R the biological rate of change.

$$\frac{\delta O_2}{\delta t} = A_z \frac{\delta O_2}{\delta z} + R \qquad (5)$$

Coefficients of eddy conductivity computed from heat budget data on a Birgean basis were used on the assumption that the coefficients of diffusivity and conductivity were of the same magnitude. In computing $\delta O_2/\delta t$

TABLE 3. *Values of the biological rate of oxidation* (R) *at various depths and pertinent information pertaining to the calculations*

Depth (m)	Volume ×10⁶m³	Area ×10⁵m²	A_z (g/cm/sec)	$\bar{O}_2$ (g/m³)	$\frac{\delta O_2}{\delta z}A_z$ (g/m²/day)	$\frac{\delta O_2}{\delta t}$ (g/m²/day)	R (g/m²/day)	R (g/m³/day)
S–3	416	1424	0.395	9.35	–0.068	–0.829	–0.897	+0.068
3–6	375	1306	0.543	9.29	–0.352	–0.843	–1.195	+0.044
6–9	324	1150	0.416	8.90	–0.604	–0.896	–1.500	–0.089
9–12	275	976	0.434	8.28	–0.518	–0.954	–1.472	–0.154
12–15	228	826	0.295	8.09	–0.268	–0.960	–1.228	–0.101
15–18	188	673	0.185	7.67	–0.181	–0.984	–1.165	–0.102
18–21	159	563	0.127	7.41	–0.085	–0.966	–1.051	–0.084
21–24	134	483	0.133	7.21	–0.049	–0.900	–0.949	–0.087
24–27	113	396	0.149	7.15	–0.003	–0.838	–0.862	–0.087
27–30	96	346	0.122	7.20	+0.021	–0.701	–0.701	–0.071
30–33	78	283	0.123	7.27	–0.034	–0.581	–0.615	–0.061
33–36	60	226	0.139	7.01	–0.090	–0.468	–0.558	–0.073
36–39	19	167	0.146	6.82	–0.116	–0.377	–0.493	–0.123
39–42	20	130	0.141	6.46	–0.077	–0.377	–0.454	–0.061
42–45	18	90	0.179	6.34	–0.143	–0.377	–0.520	–0.082
45–B	27	55	0.166	5.90	–0.211	–0.370	–0.581	–0.118

the rate of change at the top of a stratum and that at the bottom of a stratum were averaged. The average rate of change in each stratum was multiplied by the volume of the respective stratum. Starting with the lowermost stratum an accumulative sum was prepared of the daily amount of apparent oxygen consumption. The total amount consumed below the upper plane of each stratum was divided by the area of the upper plane, thus converting $\delta O_2/\delta t$ to a surface area basis. The results are entered in Table 3.

The values of A_z apply to the average value at the uppermost plane of each stratum. With the exception of the surface and bottom strata, the values were computed by averaging the value of A_z in the plane in question with values of A_z at 1-m and 2-m distances above and below the plane in question. For the surface values an average of the surface, 1-m, and 2-m values was used. For the bottom an average of the values below 45 m was used.

The oxygen gradient $\delta O_2/\delta z$ through the upper plane of each stratum was computed by taking the average of the gradient through the stratum above and the gradient of the stratum below the plane in question.

Values of R on a surface area basis were obtained by summing $\delta O_2/\delta t$ and $A_z \delta O_2/\delta z$. These were converted to a volume basis in the following manner. The surface area rates of R were multiplied by the area of the upper plane of the respective stratum. The amount of daily oxygen consumption in each stratum was determined by subtracting the amount consumed in all strata below the lower plane of the stratum in question from the amount consumed below the upper plane of the stratum in question. This difference was then divided by the volume of the particular stratum.

Oxygen production exceeded oxygen consumption in the upper 6-m zone. On the basis of the slope of R plotted against Z the compensation point would be at the 5.5-m depth. Below this depth oxygen consumption exceeded oxygen production, reaching a maximum of 0.154 g O_2/m^3/day in the 9- to 12-m zone. The rate then decreased with depth, becoming minimal (0.061 g O_2/m^3/day) in the 30- to 33-m zone. Below 33 m, R was higher; however, there was considerable variation between individual values. This may be due to the lack of accurate morphometric information in the region below 36 m, which necessitated determining volumes and surface areas by interpolation. The average value of R below 36 m amounted to 0.091 g O_2/m^3/day which was considerably higher than the values in the metalimnion.

TABLE 4. *Chlorophyll and seston concentration at various depth zones compared with rates of oxygen consumption per unit chlorophyll and seston*

Depth	Seston (g/m^3)	Chl (mg/m^3)	Oxygen (g/g seston/day)	Oxygen (g/mg chl/day)	Chl seston (mg/g)
Surface–7.6 m	2.23	8.02			3.59
7.6–15.2	1.34	6.58	.084	.017	4.91
15.2–22.8	1.84	3.67	.049	.025	1.99
22.8–30.5	1.41	2.48	.052	.029	1.76
30.5–45.0	1.94	3.06	.047	.030	1.58

It will be noted that when average oxygen concentrations are compared with R values, there was a metalimnetic oxygen maximum in the region between 27 and 33 m which would be expected if R was minimal in this region where A_z was virtually constant.

The question arises as to why R should be minimal in the metalimnion. It might be argued that the more oxidizable fraction of the seston is oxidized before particles sink to the level of the metalimnion. Reference to Table 4 indicates that the rate of oxidation of seston in the upper epilimnion, 7.6–15.2 m, was indeed higher than at greater depths. However, below 15.2 m the rate became almost constant, averaging 0.049 g O_2/g seston/day, which is nearly identical to the average rate of areal relative deficit per unit seston (0.048) that can be computed from Hutchinson (1957, Table 78).

The explanation for the minimal value of R in the metalimnion may be purely physical. If higher values of A_z were present in the hypolimnion or epilimnion than in the metalimnion, one would expect particles to sink through the metalimnion at a faster rate and thus have less opportunity to be oxidized. The vertical distributions of both seston and chlorophyll suggest this since the

concentrations of both were higher in the lowest zone, 30.5–45 m, than in the zone immediately above.

PRIMARY PRODUCTION

If it is assumed that the euphotic zone is the source of organic matter oxidized in the dysphotic zone, an estimate of this fraction of primary production can be made. Oxygen consumption below 9 m amounted to 1.472 g O_2/m^2/day. Since the surface area of the 9-m plane is 976×10^5 m^2, total daily respiration would be $976 \times 10^5 \times 1.472 = 1436 \times 10^5$ g O_2/day. With a euphotic zone surface area of 1424×10^5 m^2, a rate of production equivalent to $1436/1424 = 1.01$ g O_2/m^2/day would satisfy the dysphotic zone oxygen consumption. This figure is only an estimate of the excess of production over total community respiration in the euphotic zone.

A conservative estimate of euphotic zone respiration can be obtained if it is assumed that the rate of respiration in the euphotic zone is equivalent to that in the 9- to 12-m stratum which is apparently below the depth of effective photosynthesis and that all the organic matter formed is oxidized within the water column. A minimal estimate of gross production would be obtained by adding euphotic zone respiration to dysphotic zone respiration. On this basis, respiration in the euphotic zone would be $0.154 \times 1115 \times 10^6$ divided by $1424 \times 10^5 = 1.21$ g O_2/m^2/day. Adding this to the dysphotic zone oxygen requirement of 1.01, gross production would be 2.22 g O_2/m^2/day.

Both seston and chlorophyll values are higher in the euphotic zone, however. If the same rate of respiration per unit seston or chlorophyll could be assumed to apply as it does in the 9- to 12-m zone, euphotic zone respiration could be computed on this basis. For seston this would amount to 0.115 g O_2/g seston/day and 0.023 g O_2/mg chl/day for chlorophyll. The rate for chlorophyll is nearly equivalent to 0.033 μmole O_2/μg chl/hr determined from bottle experiments by Wright (1959).

On a seston basis, respiration in the surface to 9-m zone would amount to 2.01 g O_2/m^2/day and on a chlorophyll basis, 1.44 g O_2/m^2/day, respectively. When dysphotic zone respiration is added the estimate of gross production becomes 3.02 and 2.45 g O_2/m^2/day, respectively.

These figures may be compared with estimates of primary production made from bottle experiments during the summer of 1958 (Wright 1959). The average hourly rate of 12 series of 6-hr exposures was 0.25 g O_2/m^2/hr. Assuming a 12-hr period of photosynthesis, gross photosynthesis would have been 3.00 g O_2/m^2/day which is nearly identical to the value of gross production computed on the basis of seston.

Though limited by the validity of such crude approaches, the data suggest that gross production was not less than 2.22 g O_2/m^2/day. The evidence does not indicate that the black-and-white bottle method overestimated gross production, as claimed by Steemann-Nielsen (1954).

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THE SEASONAL VARIATION OF PHOSPHATE, SILICATE, AND NITRATE IN WATERS OF THE ENGLISH LAKE DISTRICT[1]

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ABSTRACT

A record is presented of two years continuous observations, from January 1958, to March 1960, of the north and south basins of Windermere, Esthwaite Water, and Blelham Tarn. The changes in phosphate concentration together with data for silicate and nitrate are shown. Rainfall, temperature, and total diatom population are also included. An improved method for the determination of phosphate has made possible the recognition of a vernal decline and subsequent autumnal increase in the concentration of this constituent. The changes in the chemical composition of the water are attributed to the influence of conditions in the catchment area rather than changes in the lake itself.

INTRODUCTION

The localities of the 4 lakes are shown in Figure 1. Windermere north basin receives drainage from an area of hard non-calcareous rocks. The total ionic concentration of the water averages 0.51 meq/L (milli-equivalents per liter). The south basin drainage system is influenced by the outflow from Esthwaite Water and the average total ionic concentration is a little higher at 0.55 meq/L. The drainage basins of Esthwaite Water and Blelham Tarn are situated in areas of more intensive cultivation where the rocks are softer and more weathered. The average total ionic concentrations are 0.75 and 0.80 meq/L respectively.

METHODS

Sampling: Water samples were taken each week from the upper 5 m of the lake. These were obtained by lowering a 5-m length of P.V.C. hose, approximately 20 mm in bore, into the water from a boat. The lower end of the hose was securely fastened to a 2-kg lead weight to which a thin nylon cord was attached. When the hose was fully extended the upper end was closed between finger and thumb and the lower end could then be raised by means of the cord. The column of water, about 1 L in volume, represented an average sample of the upper 5 m of the lake. In each case the sample was taken over the deepest part of the lake. This method of sampling was devised by Lund (1949).

Chemical analyses: All measurements of optical density were made with a Unicam S.P. 500 spectrophotometer.

Phosphate: Previous workers have pointed out the difficulties in attempting to store samples before analysis for phosphate (Harvey 1948, Murphy and Riley 1956). In order to obtain an accurate estimation of the phosphate in solution in the lake it was found necessary to centrifuge the sample as soon as possible after collection and then proceed with the analysis immediately. A sample of 510 ml was centrifuged for 30 min at 3,000 rev/min and 200 ml were then siphoned off for the phosphate determination. As this procedure was not always feasible, it was decided to carry out a series of phosphate determinations on the centrifuged samples which had been frozen by immersing the polythene bottle in a mixture of solid CO_2 and alcohol. The samples were completely thawed just before each determination. The results showed that the frozen samples could be kept in a deep freeze cabinet for periods of up to 8 days without appreciable change in the phosphate concentration.

Reagents: All reagents were made up from A.R. chemicals and good distilled water. The concentrated sulphuric acid was redistilled.

Wash acid: 1.2 N sulphuric acid was sat-

[1] It is a pleasure to acknowledge the valuable criticisms made by Mr. H. C. Gilson and Mr. F. J. H. Mackereth. I am also indebted to Dr. J. W. G. Lund and Miss J. Hughes for the data on algal populations, to Mr. K. Shepherd, Mr. F. Prickett, and Mr. D. Cannon for the collection of the samples and to Mrs. C. J. Worthington who prepared the graphs.

FIG. 1. Map showing the geographical position of the 4 lakes studied.

urated with *n*-hexanol by shaking the two liquids together in a separator.

Acid ammonium molybdate: 10 g ammonium molybdate were dissolved in 90 ml of hot water and added to a cooled solution of 50 ml of redistilled sulphuric acid in 50 ml of water. The cold solution was made up to 200 ml.

Stannous chloride solution: 2 g hydrated stannous chloride were dissolved in 10 ml of concentrated hydrochloric acid by carefully heating in a covered beaker; after cooling, the solution was made up to 100 ml. For use this solution was kept in an all-glass syringe the tip of which had been drawn out into a capillary. A few pieces of pure tin foil were placed in the syringe and the syringe was filled so that no air bubbles were included. This solution keeps well in the syringe since no air is admitted in use.

Phosphate standard solution: 0.439 g KH_2PO_4 (100 mg P) was dissolved in 1 L of distilled water and diluted in two stages to give a working solution containing 100 μg P/L.

Precautions: All glassware was cleaned before use by standing in hot chromic-sulphuric acid mixture for several minutes followed by thorough washing. The polythene bottles were allowed to stand partly filled with wash acid and then thoroughly washed out before each determination.

The procedure was essentially the same as that proposed by Procter and Hood (1954). The sample of up to 250 ml containing not more than 4 μg of phosphate phosphorus was placed in a screw-stoppered polythene bottle. The water was saturated by adding 0.5 ml *n*-hexanol to each 100 ml of sample. 10 ml acid ammonium molybdate were then added and after mixing the solution was allowed to stand for 5 min. 15 ml of *n*-hexanol were slowly run in from a burette, the stoppers screwed down firmly, and the bottles agitated in a suitable shaking machine. In this laboratory, mixing was carried out by placing the bottles, horizontally, in a perspex cylinder approximately 7 cm in bore and 140 cm long. The cylinder was closed at each end by rubber bungs and then revolved at about 400 rev/min for 20 min. The hexanol was then transferred to a 100-ml separator, 25 ml of wash acid added and after shaking, the two layers were allowed to separate and the aqueous layer discarded. This washing step was repeated and the aqueous layer again removed. 10 ml of distilled water, previously saturated with *n*-hexanol, were added followed by 6 drops of stannous chloride solution from the all-glass syringe. The separator was shaken for 30 sec and the two layers were allowed to separate. The aqueous layer was run off and the acid wash repeated. The hexanol layer was cleared by shaking with 1 ml of isopropyl alcohol; any remaining drops of water were allowed to

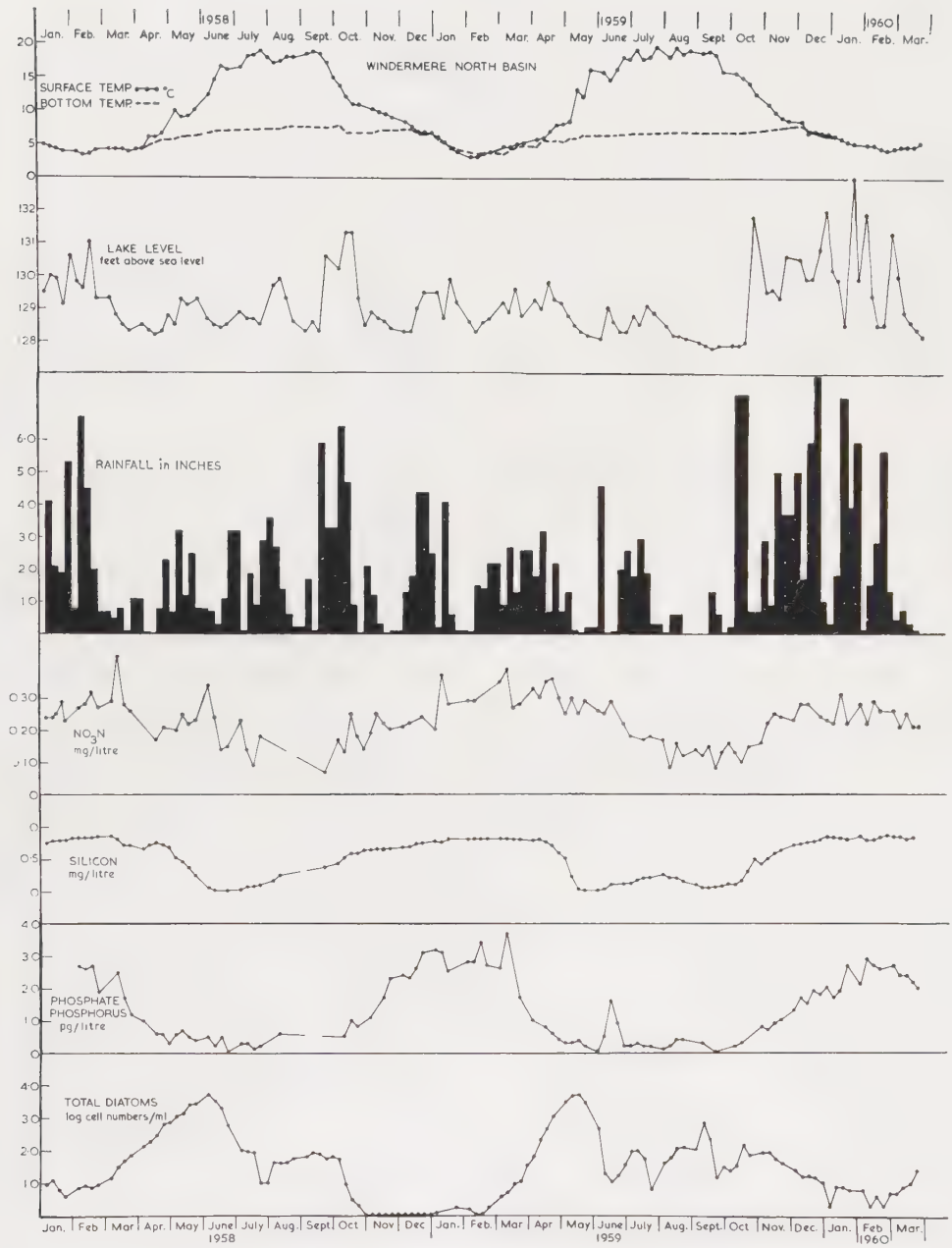

FIG. 2. Windermere north basin. Variation with time of water temperature, lake level, rainfall, nitrate nitrogen, silicon, phosphate phosphorus, and total diatom population.

collect at the bottom of the separator and then run off together with a small quantity of hexanol which served to wash out the stem of the separator. The remaining hexanol was run into a dry centrifuge tube and centrifuged for about 1 min at approximately 2,500 rev/min. At this stage the hexanol was bright and clear. The optical density was read at 730 mμ in a 4-cm cell against a blank similarly prepared. The phosphate concentration was read off from a calibration curve prepared in the manner described above

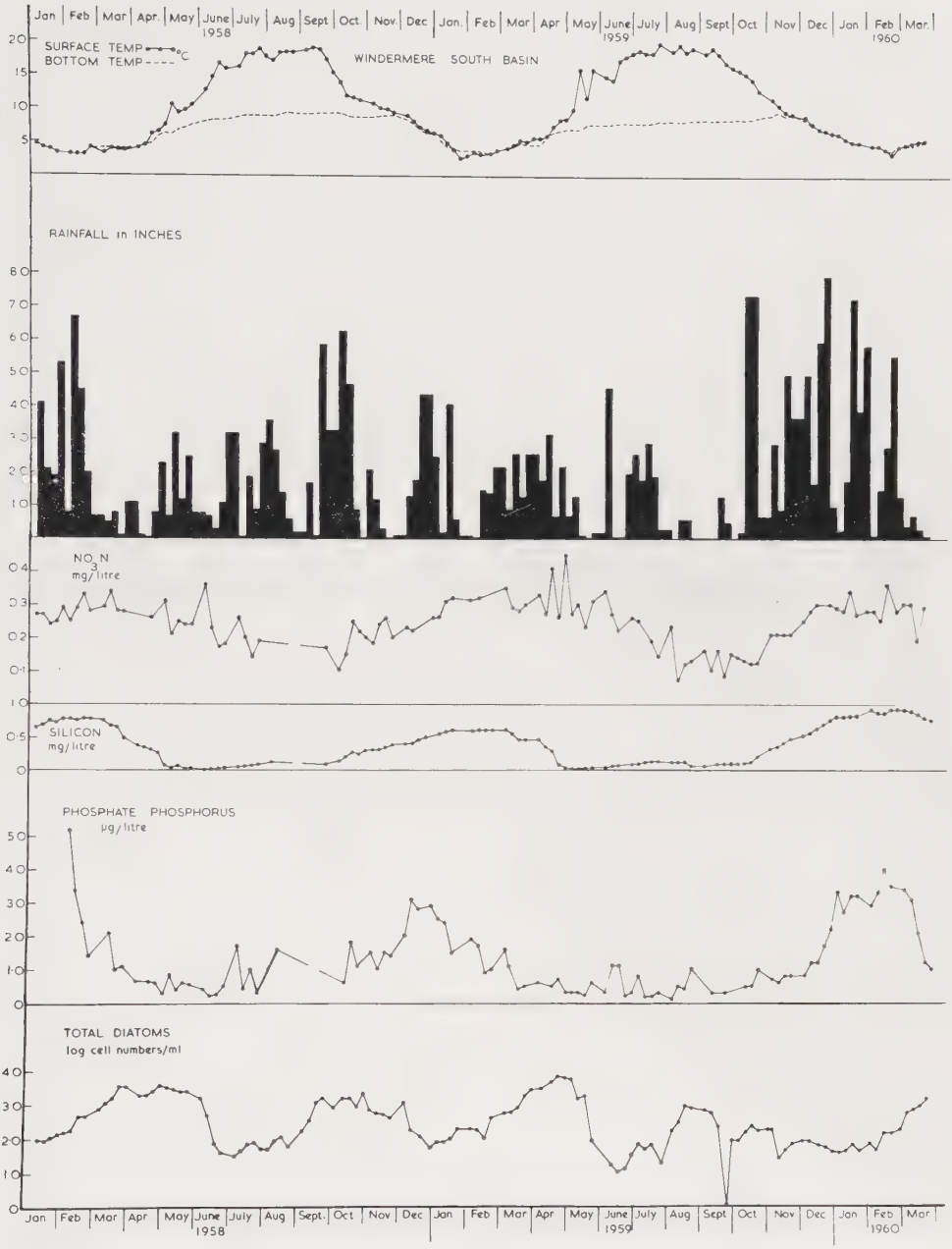
Jan Feb Mar Apr May June July Aug Sept Oct Nov Dec Jan Feb Mar Apr May June July Aug Sept Oct Nov Dec Jan Feb Mar
1958
1959
1960
SURFACE TEMP
BOTTOM TEMP °C
WINDERMERE SOUTH BASIN
RAINFALL in INCHES
NO3 N mg/litre
SILICON mg/litre
PHOSPHATE PHOSPHORUS µg/litre
TOTAL DIATOMS log cell numbers/ml

FIG. 3. Windermere south basin. Variables with time as for Windermere north basin.

using a series of standard phosphate solutions.

Determination of silicate: The method used was described by Mullin and Riley (1955).

Determination of nitrate: The procedure is essentially the same as the one described by the American Public Health Association (1955).

RESULTS

The results are shown graphically in Figures 2–5. They reveal a general pattern of

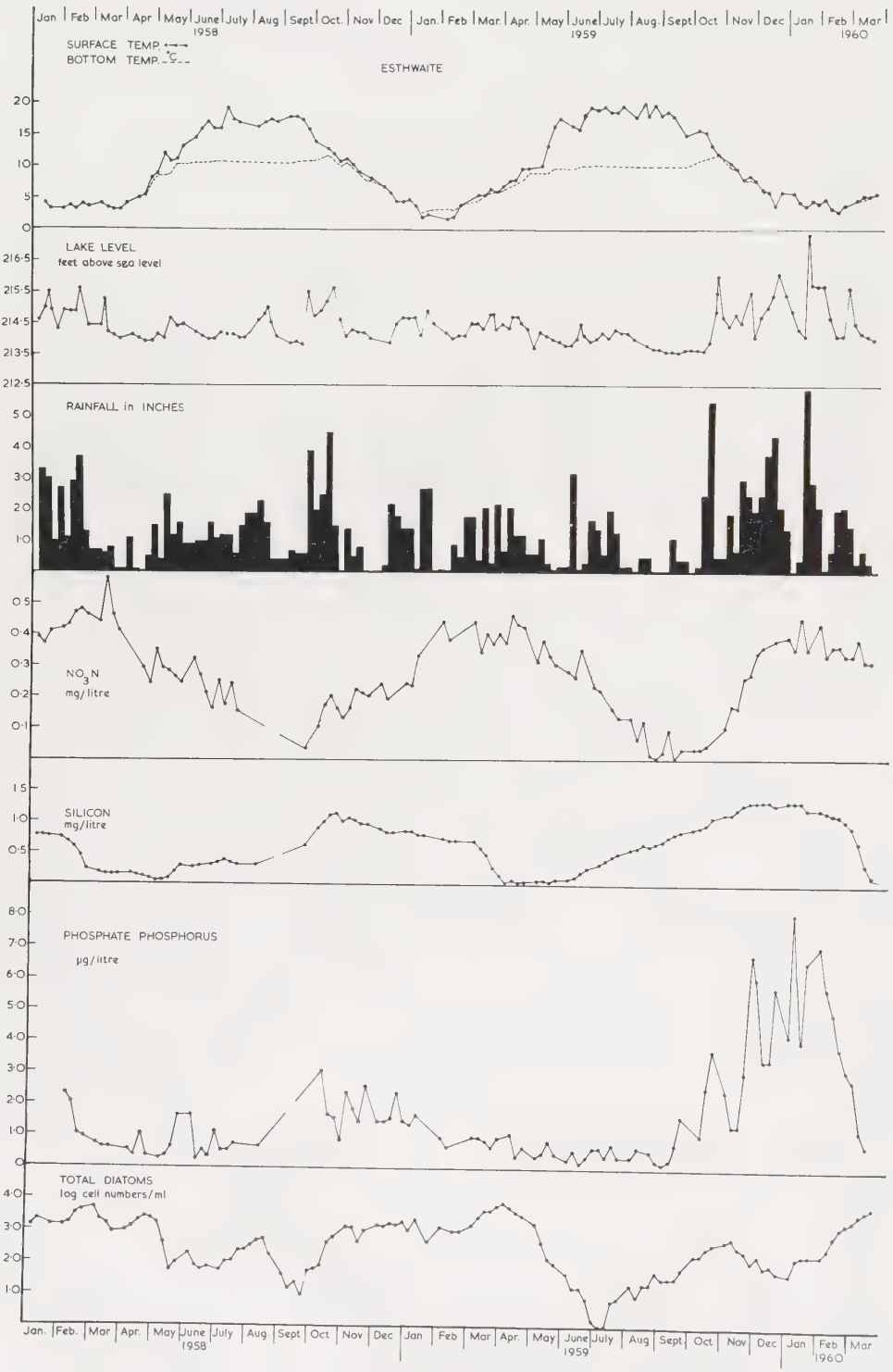

FIG. 4. Esthwaite Water. Variables with time as for Windermere north basin.

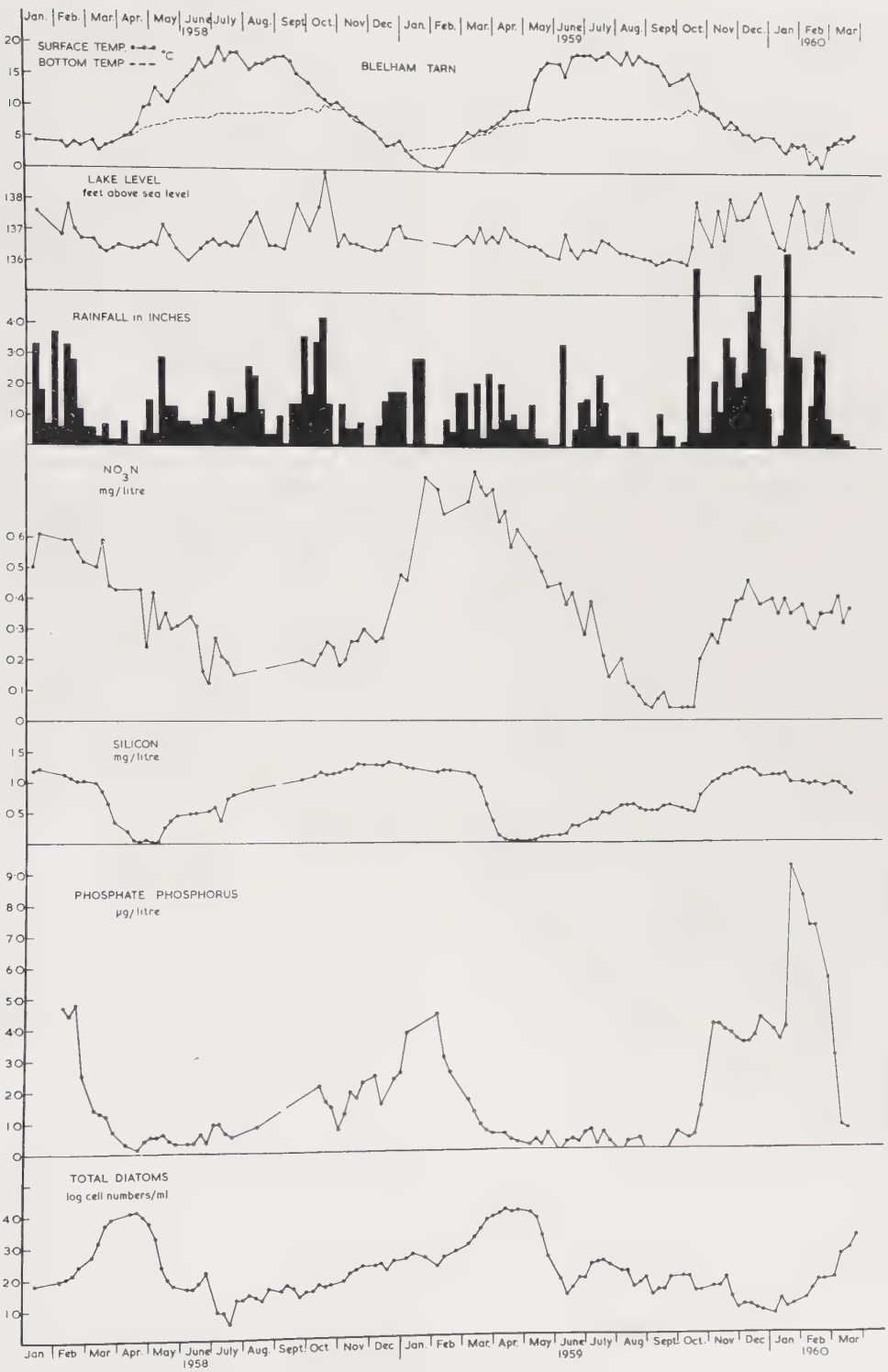

FIG. 5. Blelham Tarn. Variables with time as for Windermere north basin.

decline and increase in phosphate concentration which is followed by each lake. As the growth of plankton is directly related to the mean illumination it was expected that the decline in phosphate concentration would take place earlier in Blelham Tarn (Fig. 5), which is shallower, than in other lakes. The illuminated volumes of the 4 lakes have been worked out by Talling (1957) and the ratio of illuminated volume to total volume can be established for each lake. This ratio is practically identical for Esthwaite Water (Fig. 4) and Blelham Tarn (Fig. 5); the values are 0.64 and 0.67 respectively. The figure for Windermere north basin is 0.31 while Windermere south basin has an intermediate value of 0.40. The first indications of plankton growth and hence the removal of phosphate from the water might be expected to occur in Blelham Tarn. This expectation is not realized every year as the earliest fall in phosphate concentration took place in Windermere south basin and Esthwaite Water in January, 1959. In Windermere north basin the fall in phosphate concentration did not begin until March. It is possible that an early growth in Windermere south basin might be due to enrichment by cells brought in from Esthwaite Water.

In each case the removal of phosphate occurred before any corresponding decrease in silicate concentration. This is in agreement with Mackereth (1952) who found that phosphate was rapidly taken up in cultures of the diatom *Asterionella formosa* before any detectable growth occurred.

It will be noticed that Esthwaite Water and Blelham Tarn show great differences in phosphate concentrations between the winter months of 1958/59 and 1959/60. Thus, in Esthwaite Water the average for November and December, 1958, was 1.65 μg P/L and for November and December, 1959, 3.67 μg P/L. It is possible that this variation in phosphate concentration could be accounted for by the difference in the total diatom populations during the two periods; the averages were 1,327 cells/ml in 1958 and 256 cells/ml in 1959, a difference of roughly 1,000 cells/ml. Mackereth (1952) has shown that *Asterionella* cells in the winter can contain up to 7.0 μg P/10^6 cells. Therefore a population of 1,000 *Asterionella* cells/ml could represent the removal from the water of up to 7 μg P/L. Since the dominant diatom during the winter months of 1958 and 1959 was *Melosira*, this calculation is only valid if *Melosira* cells contain similar amounts of phosphorus.

The graphs show a marked correlation between rainfall, as measured by the lake levels, and the phosphate concentration of the surface water. The increase in phosphate concentration during the winter months of 1959 and 1960 could therefore be partly due to the much higher rainfall.

A comparative study of the autumnal changes in phosphate concentration in the different lakes yields information on the relative importance of events at the bottom and events in the catchment area at this time of the year. Mortimer (1942) showed that phosphate is released into solution from the superficial layers of the mud when a lake is stratified and the bottom water becomes anaerobic. Since this happens in Esthwaite Water but not in Windermere, the two lakes would show differences when stratification breaks down in autumn, if this phosphate from the bottom deposits were important in the cycle of the lakes as a whole. Figures 2 and 4 show no such regular differences and phosphate may indeed increase in the surface waters during summer stratification. The autumnal changes in phosphate concentration are erratic, especially in Esthwaite Water and Blelham Tarn, where high concentrations at the surface are found during floods. We may conclude that events in the bottom water are outweighed in importance by events in the drainage basin, where the application of fertilizers to agricultural land may greatly affect the surface waters of a small lake like Blelham Tarn, although, as Lund (1959) has shown, such changes are often transitory.

During the spring the removal of phosphate from the water takes place before any depletion of the silicate can be observed, but the relations between the two substances are different later in the year. In Blelham Tarn, silicate rose steadily from May to August,

1959, and then remained more or less steady until October. By contrast, the phosphate concentration never exceeded 0.6 μg P/L from 4 May to 19 October. The diatom population fell from 223 cells/ml in July to 47 cells/ml in October; thus from July to October, 1959, the phosphate must have been used by phytoplankton other than diatoms, or by the attached vegetation. This sequence of events was repeated in Esthwaite Water in 1959 but neither lake showed this result in 1958. In Windermere the increase in silicate concentration coincides approximately with that in phosphate concentration in both years. This would be expected since diatoms in Windermere form the larger part of the plankton in summer and autumn.

Having observed the regular fall in phosphate concentration during February and its subsequent erratic rise in the autumn, it is relevant to seek an explanation of the sharp fluctuations in phosphate concentration during the intervening months. The correlation between phosphate concentration and lake level indicates that the increases could be brought about simply by inflow from the drainage basin. An increase in concentration could also be caused by the release of phosphate from dead cells after a rapid decrease in diatom population. This is illustrated by the peak on 16 June, 1959, found only in the north and south basins of Windermere; it is possible that this particular sample was taken before any appreciable settling had taken place. A similar explanation could be suggested for the rise in phosphate concentration on 1 July, 1958, in Windermere south basin. Other erratic changes in summer could be related to the series of crops of non-diatom algae. Variations in the phosphate content of surface samples might also be due to a non-uniform distribution of zooplankton excreta in the samples and to changes in the populations of bacteria.

The nitrate concentration follows the same general pattern from year to year. Its removal begins after the depletion of silicate but the variations in the concentration show that other factors are involved. The irregular rises in nitrate concentration are often common to the 4 lakes; for example, the peak on 11 March, 1958, clearly reversed the downward trend at that time and was shown by all 4 lakes. The increase on 28 April, 1958, was also common although less pronounced in Windermere north basin. Again, the rise in nitrate concentration in Blelham Tarn on 30 June, 1958, ended the steady fall of the previous 3 weeks, and occurred simultaneously in Esthwaite Water and the two basins of Windermere. The lack of information concerning the other forms of nitrogen in the water makes it uncertain whether this synchronization is fortuitous.

SUMMARY

The sensitivity of the colorimetric method used for the determination of phosphate has been improved so that concentrations below 1 μg P/L can be determined. Errors due to the storage of the samples are largely avoided by centrifuging the sample as soon as possible after collection. The use of this method has made possible the recognition of a seasonal variation in phosphate concentration in 4 different lakes. The vernal decrease in phosphate concentration occurring in February or earlier takes place in all 4 lakes before any appreciable decrease in silicate concentration. The sudden increases in phosphate concentration during the summer months may be caused by: a) temporary enrichment of the surface water brought about by heavy rainfall in the drainage basin; b) the release of phosphate from dead cells after an algal "bloom"; c) contamination by zooplankton excreta.

The autumnal rise in phosphate concentration can be erratic and at this time of the year the situation is confused. In addition to the increases in phosphate concentration brought about by the factors already mentioned, it is possible that phosphate is released from the bottom deposits when the hypolimnion has been deoxygenated for a period. It is noted however that increases in phosphate concentration sometimes occur when the lakes are stratified.

The erratic variation of the nitrate concentration during the year is demonstrated but no explanation is offered to account for the variations.

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THE VERTICAL VARIATION OF WIND-DRIVEN CURRENTS IN LAKE MENDOTA[1]

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ABSTRACT

The deviation of wind-driven water currents from wind direction was examined as a function of depth in Lake Mendota utilizing the free-drag method. The mean vector hodographs were obtained for various wind velocities. The relation of wind velocity to angular deflection was also obtained.

The depth of frictional influence was empirically determined to be between 2 and 3.5 m and an improved relationship with wind speed was developed.

Wind stress on the water surface was calculated by fitting Ekman and Rossby spirals to the hodographs and integrating the cross-wind component from the surface to depth D. The proportionality of the stress to the wind velocity was determined and comparisons made with previous computations.

INTRODUCTION

The basic problem in the determination of the rotation of water currents relative to the wind has been predominantly the lack of a sufficient number of observations. Theoretical work, therefore, has proceeded with almost negligible empirical verification.

It has been shown theoretically by Ekman (1905) that, in a body of water of constant viscosity and great depth, the surface current should be deflected 45° to the right of the wind. The angle of deflection should increase regularly until a depth is reached where the current is opposite to that at the surface. This level (D) is known as the depth of frictional influence. The current velocity, according to Ekman's results, decreases exponentially with increasing depth and at D is equal to $e^{-\pi}$ times the surface velocity.

In further theoretical studies Rossby and Montgomery (1935) utilizing an eddy viscosity dependent upon a varying mixing length, determined that the deflection of the surface wind-driven currents at latitude 5° increases from 35° at a wind of about 12 mph to 43° at a wind of 48 mph, and at latitude 60° from 42° to 53°.

Woodcock (1943) in his studies of wind-induced motion of *Physalia* (Portuguese Man-of-War) found no deflection of wind-driven surface water currents from wind direction. Drift bottles placed in a line at right angles to the wind regrouped themselves in lines parallel with the wind direction and at right angles to the initial line of distribution. Apparently the convergence found at the foam lines was sufficient to overcome the general Coriolis deflection and the drift bottles floated with the wind rather than to the right of the wind.

It is the purpose of this report to determine empirically the magnitude of the deflection of lake-water currents from wind direction and to discuss the significance of the results in light of previous empirical and theoretical work.

Currents in Lake Mendota were measured initially at a tower erected to take meteorological data and located 492 m north of Second Point, and also at a fixed buoy located near the center of the lake (Fig. 1). The majority of measurements were taken at the buoy because of its centrally located position and greater water depth.

Measurements were made between June 7 and August 26, 1960, on days favorable to accurate measurements. Data were not taken when the winds were very light and variable or were backing or veering rapidly.

On August 8, 1960, an experiment was performed to determine whether to eliminate data accumulated under variable wind con-

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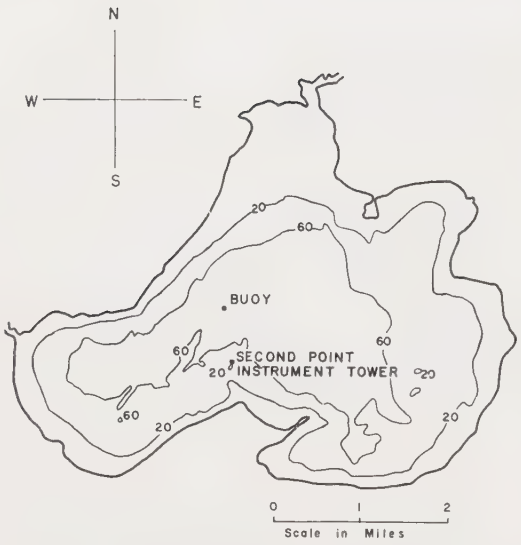

FIG. 1. Lake Mendota, showing regions of data collection and experimentation. Contour lines are in feet.

ditions. On this day, the wind was initially very light and mostly from the southwest. At 11:25, a frontal passage caused the wind to veer to the northwest at approximately 8.0 mph. Under these conditions the effect of shifting winds on the currents at the various levels could easily be determined. The surface current appeared to respond almost instantaneously to the wind shift, the 20-cm current in 20 min while the 200-cm current required 90 min.

Accurate measurements were not possible when winds were greater than about 15 mph. Seven hundred and seventy-six individual measurements were made.

If the only currents present in the lake were those caused by the wind, the current velocity at the depth of frictional influence would be negligible. At this depth, however, the observed current varied between 0.36 and 0.60 times the surface current. This current is the slope or gradient current and is due to the slope of the water surface related to the unequal distribution of mass. Since the slope current is independent of depth this component of the current is vertically uniform.

The relative or thermal current is dependent on the relative field of density and therefore varies with depth. It can, however, be calculated from the mean horizontal temperature gradient in the layer under observation.

Water temperature observations were taken periodically during the period of experimentation and it was found that the horizontal temperature gradient in the upper 3 m was not more than .01°C per km. With such a small temperature gradient the relative current did not exceed 1 cm sec^{-1} variation within the frictional layer.

Another type of current present in Lake Mendota is the oscillatory seiche current, whose period is determined by the dimensions of the lake. Because of the oscillatory nature of the seiche current its effect on wind-driven currents may be eliminated by taking observations over the entire seiche period. Since the seiche period in Lake Mendota is 25.6 min for the N–S axis and 25.8 for the E–W axis (Bryson 1952) measurements were taken over a period varying from 25 to 26 min.

INSTRUMENTS AND DATA COLLECTION

Currents were measured at the following depths: surface to 10 cm, 10–20 cm, 20–30 cm, 50–60 cm, 95–105 cm, 145–155 cm, 195–205 cm, and 295–305 cm. The free drags employed in the measurements were constructed from two 0.040 in. aluminum plates (10 cm × 30 cm) held at right angles by small angle braces. They were suspended from the float by 50-lb test nylon cord attached to two leaders (Fig. 2).

The drags were supported by 10-oz polyethelene bottles and small metal cans of similar size. The area of the float exposed above the water surface was small in relation to the drag area, the ratio being approximately 1:20, so that the direct effect of the wind on the float and on the observed drag movements was small.

The boat used was equipped with a centrally located compass with which the direction to the buoy could be read with a maximum error, in rough water, of approximately ±2°. A taffrail log calibrated with a coefficient of variation of ±3.6% was employed to measure the distance the drag moved from

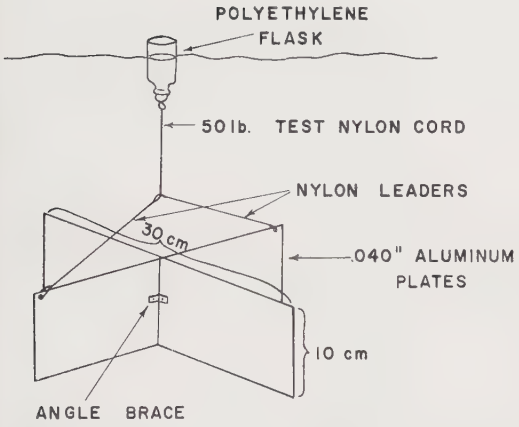

FIG. 2. Free drag employed for measuring currents.

its initial position. Therefore, a current measured at 10 cm sec^{-1} would have an error of ± 0.36 cm sec^{-1}, while the directional error would amount to $\pm 2°$.

Wind direction and velocity were measured at the meteorological tower located on Second Point Bar, 457 m north of Second Point. The three-cup anemometer and wind vane were 5.5 m above mean lake level. Observations were taken every 5 min and transmitted to shore where they were automatically punched on IBM cards.

The final wind data were evaluated by averaging the 5-min observations over the total time of measurements.

DEFLECTION OF CURRENTS

This empirical study indicates the existence of progressive turning with depth of wind-driven currents in Lake Mendota. The greatest deflections occur at intermediate wind speeds (5.0–9.9 mph). At lighter wind velocities (0.0–4.9 mph) the deflections are slightly less but are further decreased at higher winds (10.0–14.9 mph) (see Fig. 3). The mean deflection for all records was 20.6° to the right of the wind.

Figures 4, 5, and 6 are the hodographs for the following wind classes, 0.0–4.9 mph, 5.0–9.9 mph, 10.0–14.9 mph, while Figure 7 is the average hodograph. Table 1 lists the corresponding hodograph values.

Rossby's (1932) theoretical average surface deflection of 38.5° for winds of 12 mph is larger than the present empirical result. The present study indicates that at wind velocities of 10–15 mph the surface deflection is only 15.6°. The maximum surface deflection (16.0°) occurred at wind velocities between 5.0 and 9.9 mph.

Witting (1909), in his studies on Lake Ladoga, using 109 observations found an average surface deflection of 33° to the right of the wind. Fjeldstad (1929) suggested that such a large angle might be explained by a vertical gradient in eddy viscosity.

Witting also found that the angle between the wind and the current decreased with

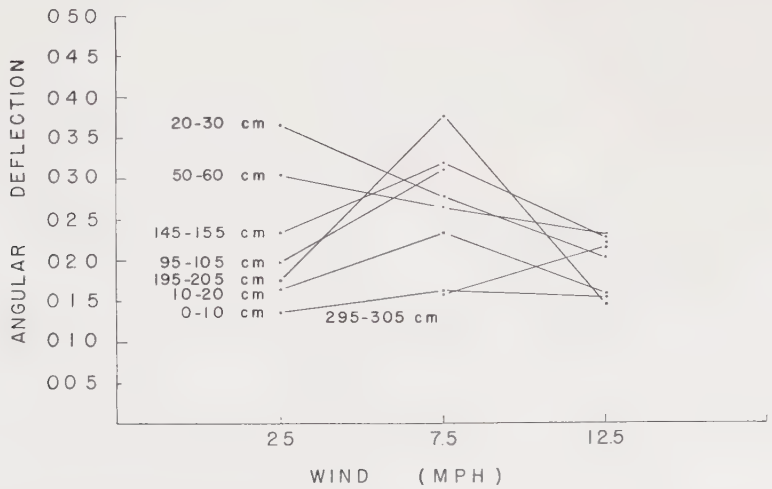

FIG. 3. Angular deflection of currents as a function of depth for winds of 2.5, 7.5, and 12.5 mph.

TABLE 1. *Angular deflection in degrees (θ), water current speed as measured in cm sec^{-1} (V), and number of cases studied (N), as a function of depth in cm for indicated classes of wind speed in mph*

Depth	0.0–4.9 mph			5.0–9.9 mph			10.0–14.9 mph			Average		
	θ	V	N	θ	V	N	θ	V	N	θ	V	N
0– 10	13.3	9.91	17	16.0	10.52	34	15.6	14.63	35	15.3	12.34	86
10– 20	16.3	9.55	15	23.1	9.50	37	15.8	13.11	32	19.1	10.87	84
20– 30	36.4	7.92	9	27.9	8.28	29	20.2	13.26	27	25.9	10.26	65
50– 60	30.1	7.87	11	26.4	8.08	25	23.1	11.84	19	26.0	9.40	55
95–105	19.8	6.20	11	31.0	8.13	27	22.4	12.19	23	25.6	8.94	61
145–155	23.2	4.22	9	31.8	6.96	24	22.6	11.63	24	26.7	8.48	57
195–205	17.5	3.56	12	37.5	6.91	19	14.3	10.21	20	23.7	7.37	51
295–305	–44.7	0.91	3	15.9	5.13	20	21.5	8.84	24	15.8	6.71	47

increased wind. This result is in agreement with the present study.

Figures 4 to 7 indicate the existence of a progressive rotation with depth. Connecting the vector endpoints, curves are formed approximating spirals. These "spirals" differ from Ekman's theoretical model in that they are not exponential. All deflections are to the right of the wind and form reasonably smooth curves, except for the hodograph for higher wind velocities.

The flattening of the spiral, in this particular instance, appears due to increased wave action. Munk (1943) has shown that at wind speeds below about 12.5 mph the water surface is hydrodynamically smooth. Furthermore, according to Munk, the Kelvin-Helmholtz theory shows that instability first occurs at a wind speed which corresponds to the critical speed for the transition from a hydrodynamically smooth to a hydrodynamically rough water surface. The presence of

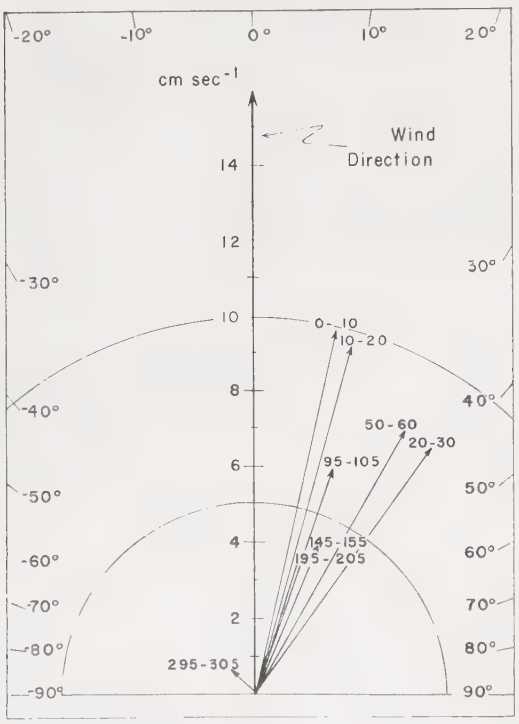

FIG. 4. Hodograph of currents at wind velocities between 0.0–4.9 mph.

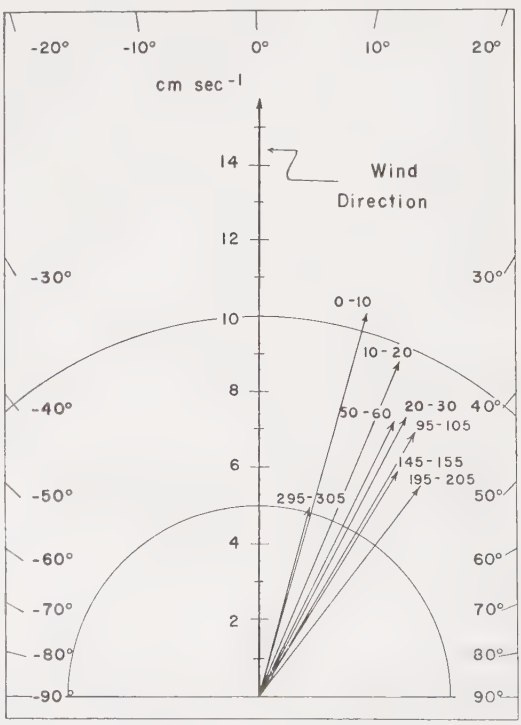

FIG. 5. Hodograph of currents at wind velocities between 5.0–9.9 mph.

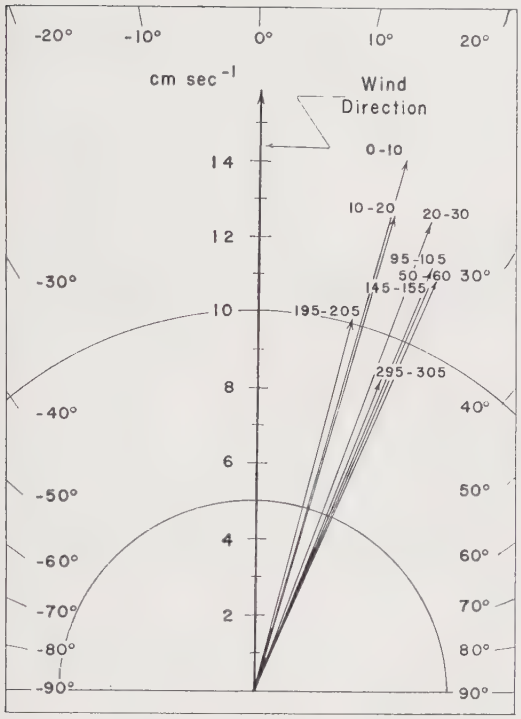

FIG. 6. Hodograph of currents at wind velocities between 10.0–14.9 mph.

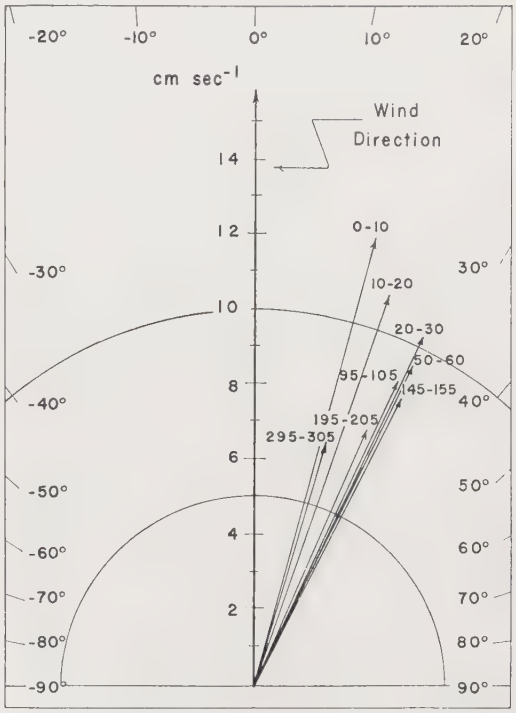

FIG. 7. Hodograph of currents at all wind velocities.

whitecaps, which were observed with winds of about 10 mph, is the most obvious evidence of the transition to instability and turbulence. This increased turbulence is the apparent cause of the distortion of the current spiral at wind velocities above that critical value.

Similarly, Rossby (1936) has shown that at wind velocities below 10 mph the water surface has the character of a smooth surface and wind profiles indicate the existence of a laminar sublayer. At wind velocities greater than this critical value the stress of the wind on the water surface increases rather abruptly by about 200% and the laminar sublayer disappears (Sverdrup, *et al.* 1946). The present empirical results indicate some such change.

Fitting Ekman and Rossby spiral solutions to the empirical vectors (Fig. 8) allows for the determination of the depth of frictional influence as well as the magnitude of the current at that level. The corresponding values are given in Table 2.

Hutchinson (1957) discusses two theoretical formulae for the calculation of the depth of frictional influence. Both expressions contain the wind velocity as the only variable for an individual lake. The first relationship

$$D = \frac{7.6\,W}{\sqrt{\sin \Phi}} \qquad (1)$$

was developed by Ekman (Hutchinson 1957), the latter

$$D = \frac{3.67\sqrt{W^3}}{\sqrt{\sin \Phi}} \qquad (2)$$

by Thorade (1914). In the above formulae W is wind velocity in m sec^{-1} and Φ is the latitude. At wind velocities below 4.3 m sec^{-1} Thorade's formula gives lower values of D than does Ekman's.

Assuming that $\sqrt{\sin \Phi}$ is a valid parameter, the following relationship fits the data more realistically.

$$D = 1.5\sqrt{\frac{W}{\sin \Phi}} \qquad (3)$$

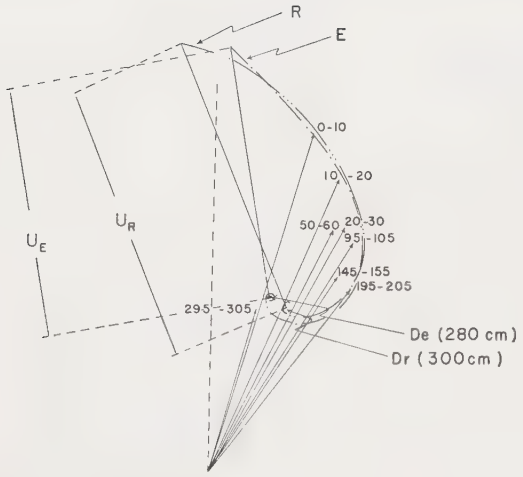

FIG. 8. Ekman spiral (E) and Rossby spiral (R) fitted to mean current vectors at winds of 5.0–9.9 mph, showing manner in which U and D are determined.

Utilizing this expression D values calculated for wind velocities averaging 2.5, 7.5, and 12.5 mph are given in Table 3.

These results are significantly closer to the values found in the present empirical study than those computed from the first two expressions. Table 4 lists the values for comparison purposes.

SURFACE STRESS

Surface stress values were calculated by integration of the spiral solutions of both Ekman and Rossby. The main differences between the two solutions is that Ekman assumes a constant eddy viscosity while Rossby considers a parabolic decrease with depth.

The two components of the water current

TABLE 2. *The depth of frictional influence* (D) *and the current at that depth as a function of wind velocity determined from fitted Rossby* (D_R) *and Ekman* (D_E) *spirals*

Wind (mph)	D_E (cm)	D_R (cm)	Current at D_E (cm sec^{-1})	Current at D_R (cm sec^{-1})
0.0– 4.9	180	180	4.0	4.3
5.0– 9.9	280	290	5.2	5.0
10.0–14.9	330	330	7.9	7.9
Average	290	290	6.8	6.9

TABLE 3. *The depth of frictional influence* (D) *calculated from* $D = 1.5\sqrt{W/\sin\Phi}$

Wind velocity (mph)	Wind velocity (cm sec^{-1})	D (cm)
2.5	111	190
7.5	333	314
12.5	555	428

which describe the Ekman spiral are as follows

$$u = U\,(1 - \cos\beta\, e^{-\beta}) \tag{4}$$

$$v = U\, e^{\beta} \sin\beta \tag{5}$$

where U is the difference in velocity between the surface current and the current at D, and β is equal to $Z\sqrt{f/2K}$. Here Z is depth from the surface, K is the eddy diffusivity and f is the Coriolis parameter. The surface stress is then given by

$$\tau_0 = \sqrt{\tau_{x,0}{}^2 + \tau_{y,0}{}^2} \tag{6}$$

where $\tau_{x,0}$ and $\tau_{y,0}$ are the stresses in the x and y directions and

$$\tau_{x,0} = \rho K \frac{\delta u}{\delta Z} \tag{7}$$

$$\tau_{y,0} = \rho K \frac{\delta v}{\delta Z} \tag{8}$$

The values of $\delta u/\delta Z$ and $\delta v/\delta Z$ are obtained by differentiating equations (4) and (5) with respect to depth Z. Solving for $\tau_{x,0}$ $\tau_{y,0}$ and substituting these values in the equation for τ_0 the following relationship results

$$\tau_0 = \rho U \sqrt{fK} \tag{9}$$

The special level D where $\beta = \pi$ has been defined as the depth of frictional influence

$$\pi = D\sqrt{\frac{f}{2K}} \tag{10}$$

TABLE 4. *The depth in meters of frictional influence as determined from equations (1), (2), and (3)*

Wind (m sec^{-1})	Ekman D	Thorade D	$1.5\sqrt{W/\sin\Phi}$ D
1.1	10.5	4.9	1.9
3.3	30.7	26.6	3.1
5.6	50.6	57.1	4.2

Eliminating K between equations (9) and (10) we are left with a relationship from which τ_0 can be easily obtained from the present data

$$\tau_0 = \rho U \frac{Df}{\pi\sqrt{2}} \tag{11}$$

While in the Ekman spiral $K = K_0 = \text{const}$ (independent of Z) Rossby and Montgomery (1935) have shown that for K being a parabolic $f(Z)$, $K \sim (H-Z)^2$ and

$$u = U\left\{1 - \frac{H-Z}{H}\cos\left[\sqrt{2}\ln\left(\frac{H-Z}{H}\right)\right]\right\} \tag{12}$$

$$v = -U\frac{H-Z}{H}\sin\sqrt{2}\ln\frac{H-Z}{H} \tag{13}$$

where U is the same as before and H is the level at which the eddy viscosity becomes zero.

The surface stress again may be determined using equations (6) to (8). Then the eddy viscosity at $Z = 0$ may be expressed as

$$K_0 = \rho f \frac{\sqrt{2}}{6} H^2 \tag{14}$$

and the expression for surface stress is

$$\tau_0 = \rho f \frac{1}{\sqrt{6}} H U \tag{15}$$

The depth of frictional influence is determined, with the aid of (13), as

$$\sqrt{2}\ln\frac{H-D}{H} = \pi \tag{16}$$

Solving for D we find that, in terms of H

$$D = 0.8915\,H \tag{17}$$

and the surface stress as determined from the Rossby solution becomes

$$\tau_0 = 0.458\,\rho\,f\,D\,U \tag{18}$$

Comparing the two equations for τ_0 it is obvious that for a given pair of parameters D and U, the stress values determined from the Rossby expression are 2.03 times greater than those determined from the Ekman solution.

Both Ekman and Rossby spirals were fitted to 25 individual hodographs and the D and U values were determined for each of these cases. This method is illustrated in Figure 8. Once the D and U values were obtained the surface stress was computed from equations (11) and (18).

Figure 9 is a log–log plot of the surface stress in dynes cm^{-2} against the wind velocity in cm sec^{-1} and indicates the values calculated by both Rossby and Ekman solutions. The slope of the lines fitted to the data shows that τ_0 is proportional to the wind.

Stearns (1952) working on Lake Mendota determined the surface stress by two other methods. At winds greater than 800 cm sec^{-1} he assumed that the wind stress is the singular cause for the build-up of the seiche and that the total stress of the wind is used to increase the seiche amplitude. With these assumptions and using seiche records, Stearns calculated the total energy of the seiche wave and the water velocity per unit area. From this he calculated the total momentum flux into the lake. At these relatively high wind velocities Stearns found that the stress varied with the square of the wind velocity.

At winds below 800 cm sec^{-1} Stearns determined the stress by calculating the local change of momentum by direct current measurement. He assumed that the stress on the surface was constant in magnitude and direction, that horizontal divergence takes place in the direction of the surface stress, and that surface waves do not result in a change of momentum in the volume. His calculations of the stress at the lower wind velocities indicate its variation with the cube of the wind velocity.

Other empirical studies of the relatonship between the surface stress and the wind velocity have shown the stress to be proportional to the square, the cube, and other powers of the wind. The present study indicates that the stress is directly proportional to the wind. This is true for both the Ekman and Rossby spiral solutions although the latter values are approximately twice as great as the former (Fig. 9). The fact that various investigators have found the stress proportional to different powers of the wind (Wilson 1960), at similar wind velocities indi-

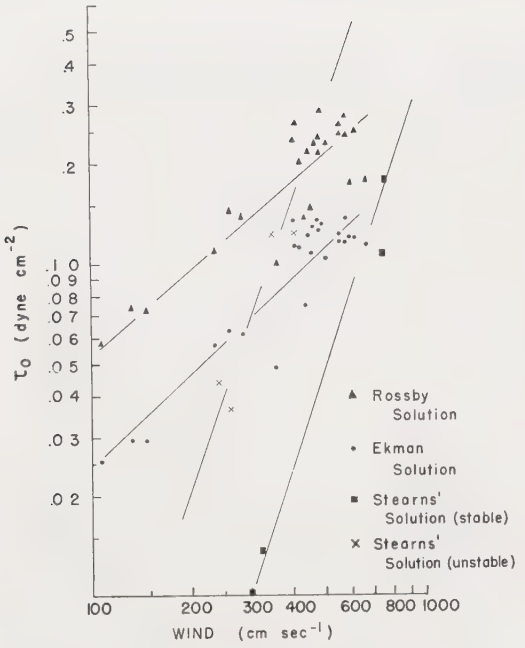

FIG. 9. Surface stress as a function of wind velocity as determined by the Rossby and Ekman spiral solution. Stearns' stress values for Lake Mendota are also included.

cates the necessity of further study of this problem.

A weakness of the present study of surface stress is that the Rossby and Ekman spirals were fitted to the hodographs by eye.

The value of D could be estimated, with reasonable accuracy, with an error of $\pm 10\%$, while U could similarly be read with an error of $\pm 10\%$. The total computational error in determining the stress is therefore $\pm 14\%$.

CONCLUSION

The present empirical results indicate the existence of a definite rotation with depth of the wind-driven currents in Lake Mendota. The average observed angle of deflection was 20.6° to the right of the wind. The deflections for all wind classes were less than the values expected according to the theories of Ekman (1905) and Rossby and Montgomery (1935).

Hodographs of the current vectors for the various wind classes (0.0–4.9 mph, 5.0–9.9 mph, 10.0–14.9 mph) indicate this progressive rotation with depth. Ekman's exponential curves as well as Rossby spirals were shown to fit the data reasonably well and allowed for the determination of D and the surface stress.

At wind velocities between 10.0–14.9 mph the deflections were more erratic than at the lower wind velocities and the resultant curve less smooth. This is probably due to the presence of a critical wind speed between 10.0–14.9 mph. This conclusion coincides with Munk's (1943) observational evidence and Rossby's (1936) theoretically derived transition between flow with a laminar sublayer and turbulent flow, occurring at winds of about 12.5 mph.

The present study indicates the depth of frictional influence to be between 1.8 and 3.3 m as opposed to previous theoretical estimates of D between 20 and 100 m. A relationship has been developed for the determination of D which places the depth of frictional influence between 1.9 and 4.3 m, in closer agreement with observations.

The stress exerted by the wind on the water surface, as computed by integration under fitted Ekman and Rossby curves, appears to vary directly with the wind (Fig. 9) at all wind velocities studied. Other investigators have found the stress to vary with the square or the cube of the wind velocity.

Figure 9 indicates that values determined by the Ekman method are of approximately the same magnitude as Stearns' (1952) computations for unstable conditions over Lake Mendota. The stress as calculated by the Rossby spiral solutions are considerably higher than Stearns' values at winds less than 350 cm sec^{-1} but are comparable at velocities between 350 and 800 cm sec^{-1}.

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AN EMPIRICAL STUDY OF WIND FACTOR IN LAKE MENDOTA[1]

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ABSTRACT

Wind blowing across a water surface will transmit momentum to the water and cause a surface current. The ratio of water velocity to wind velocity is called the wind factor. This paper presents observed values of the wind factor obtained as median values and by regression analysis of wind velocity *vs.* water velocity. The data show that the wind factor is a discontinuous function at a critical wind speed. Water velocity in the surface layers increases with wind velocity until a critical wind speed is reached, and then it decreases. This observation is in agreement with Munk's (1946) theory of a critical wind speed for air-sea boundary processes, which yields air-sea boundary instability for winds exceeding 6.5 m/sec. The observations taken in Lake Mendota yield a critical wind speed of 5.7–6.1 m/sec. The present results were arrived at after a study of 356 observations.

BACKGROUND ON THE WIND FACTOR

Since Ekman's (1905) classical paper, "On the Influence of the Earth's Rotation on Ocean Currents," various investigators have worked on the relationship of water velocity to wind velocity, *i.e.*, the wind factor. Ekman concluded that:

$$\text{Wind Factor} = \frac{v_0}{w} = \frac{0.0127}{\sqrt{\sin \phi}}$$

where (v_0) equals the surface current velocity, (w) is the wind velocity, and sin ϕ is the sine of the latitude. The formula gives a constant wind factor for a specific latitude. It yields values of 2.5% at 15° N, and 1.4% at 60° N.

Rossby and Montgomery (1935) using a different distribution of eddy viscosity with depth concluded that the wind factor decreases with both latitude and wind velocity. The values they obtained ranged from 2.3% to 3.2%.

Witting's work (1909) suggested a formula of the form,

$$v_0 = 0.48 \sqrt{w}$$

where both v_0 and w are in cm/sec.

Langmuir (1938) found a mean wind factor of about 2% in Lake George, as did Olson (1952) in Lake Erie.

Keulegan (1951), using an experimental tank, found that The Reynolds Number ($Re = (v_0 \rho z)/\mu$) could be plotted against the wind factor with the two equations:

$$\frac{v_0}{w} = 7.6 \times 10^{-4} \left(\frac{v_0 \rho z}{\mu} \right)$$

$$v_0 = 57.8 \times 10^{-8} \, (\rho \, z \, w^2)$$

where ρ is the density, μ is the viscosity, and z is the depth of the water. According to this investigation, at values of $Re = 2{,}000$ the ratio becomes a constant so that v_0 is given by $0.033w$, the velocity being independent of the depth of water in the tank. $Re = 2{,}000$ appears to occur at a current velocity of about 0.2 cm/sec for water depth of 1 m. Van Dorn (1953), using observations from an artificial pond, obtained somewhat similar results in later experimentation.

Hughes (1956) using plastic envelopes about 1 cm in diameter, measured surface currents. He found that the ratio of water movement to the gradient wind speed was 2.2%. The time interval of his measurements was quite long, ranging from 27 to 145 days. The drift distance varied from 132 to 638 miles.

The observed values of the wind factor in Lake Mendota are given in the following sections.

METHOD OF OBSERVATION

All observations included in this paper were made on Lake Mendota, 43°04′ N, 89°22′ W. The University of Wisconsin Meteorology Department has placed an in-

[1] No. 21 in the series of reports of the Department of Meteorology to the Lakes and Streams Investigation Committee of the University of Wisconsin. This research was also supported in part by the Office of Naval Research and the Army Electronics Proving Ground.

strument tower 457 m from shore off Second Point. At the time of the current observations, this tower was equipped with a wind vane and three-cup anemometer, albedo measuring instruments, and water and air thermometers. The readings from these instruments were automatically sent back to an IBM punchcard machine on shore at 1, 5, or 15-min intervals. Therefore, a nearly continuous record of the above variables was available.

The height of the anemometer above the water surface varied from 5–5.5 m dependent upon lake level. In problems involving wind-driven currents the literature often does not stress the importance of the height of the wind measuring device. In some cases the height of the anemometer is not mentioned. Investigations by Kutzbach (1960) show that there is a 10–15% change in wind speed between the levels of 2 and 10 m over Lake Mendota. Therefore, the height of the wind measuring equipment is a significant variable when one compares the observations of different investigators.

Current measurements were made by the free-drag method. Two release stations for drags were set up. One was at the tower in 2 m of water; the other was 760 m waterward, toward the center of the lake, in 20 m of water.

There was no apparent difference in the data taken at the two release points. At lower wind speeds one might not expect currents to be influenced by the lesser water depth. However, at higher winds the 2-m depth might well have an effect on the water velocity. But by chance, when the wind was 5 m/sec or more, all current observations taken near the tower were recorded while the wind direction was from the southwest or southeast. Therefore, at higher wind speeds the drags moved off the Second Point Bar into deeper water where they were not subject to bottom stress effects.

Drags were made of two plates of light aluminum fitted together at a 90° angle. The plates measured 30 cm by 10 cm, and were attached to a 6-oz milk can float. The area ratio of plates to can was on the order of 20 to 1. The drags were normally allowed to travel over a time interval of 25 or 26 min. Three hundred and fifty-six observations were made in the upper 60 cm of water.

The distance from drag release point to pickup point was measured by means of a taffrail log. This instrument has a dial fastened to the side of the boat, and a length of rigid wire leading from it into the water. The water end of the wire has two propellers attached. Motion through the water causes the propellers to turn, and the number of propeller turns is registered on the dial. Within limits, the total turns as recorded on this dial are independent of the speed of the boat. Therefore, the instrument measures distance only.

Calibration of this instrument showed that the coefficient of variation was ±3.6%.

EXAMINATION OF THE FACTORS THAT CAUSE WATER CURRENTS

The immediate wind stress is, of course, only one of several variables that will contribute to a water current at any given time. Other variables which one must consider when using data from this lake include: 1) the seiche, 2) boat-motor generated disturbances, 3) previously initiated set or gradient currents, 4) air-water temperature differences. Waves, of course, add a short-period oscillatory component.

1) The seiche is, perhaps, the most easily separated variable. Years of observations show a period of 25.6 min for the Mendota seiche. Therefore, the time interval used in the current velocity runs for this study were generally 25 or 26 min to integrate out the oscillatory seiche currents. A few of the observations were run over different periods of time because of lost drags or other incidentals. In a few cases of very slow currents the velocities were computed over a time interval of 52 min or two seiche periods.

2) Because of the method of distance measurement it was many times necessary to run the boat in close to the float. However, to nullify possible error the observations were made by coming down on one side of the drag and going back on the other. In any instance, a motor disturbance causes only slight movement of drags.

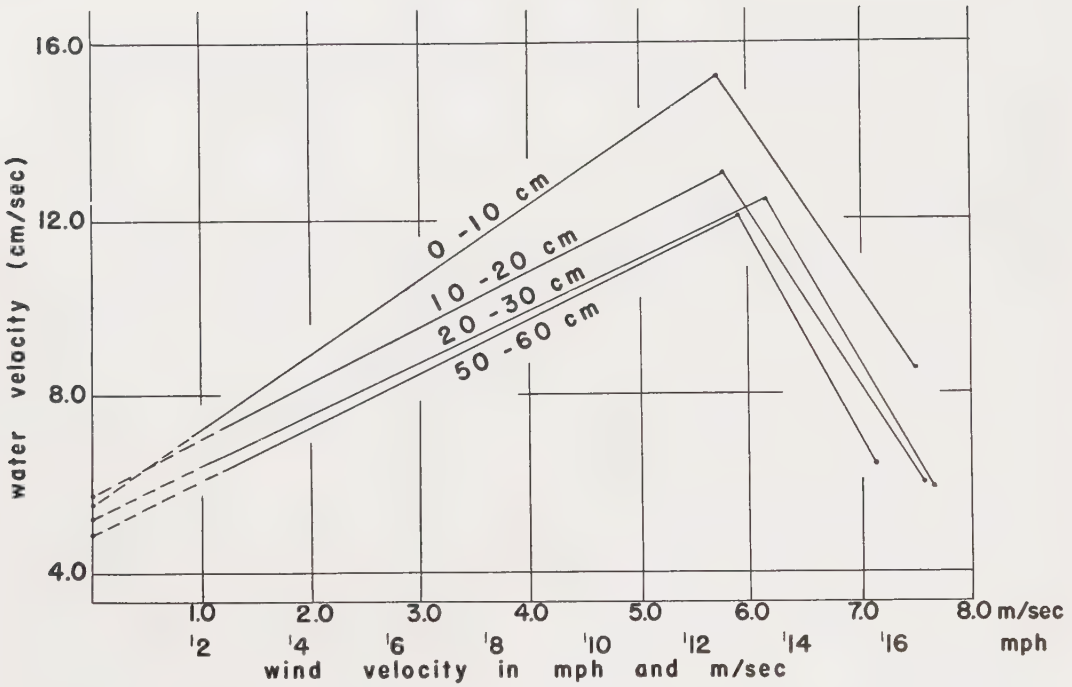

FIG. 1. Composite least squares regression lines of water velocity as a function of wind velocity. The two segments of each line were obtained by dividing the data into the wind speed ranges of 1–5.5 m/sec and 5.5–8.0 m/sec. The inflection points are the intersections of the linear regressions obtained for the two segments so defined.

3) The previously initiated current is a highly important variable in many cases. With winds below 2 m/sec it is especially significant. Apparent wind factors of 20, 30, and even 50% would appear in the data at times if the gradient currents were ignored.

The most usual cause of a gradient current involves the slope of the water surface. The slope results from unequal distribution of mass. Physical factors that may cause this situation include thunderstorms which produce unequal distribution of rain over the lake surface. Heavy runoff from the river and streams entering the lake will produce general water movement as will water discharge at the lake locks, though this factor may be shown to be negligible in Lake Mendota.

Normally, however, the wind stress causes the greatest redistribution of water mass and, therefore, the strongest currents. Consequently, after a wind shift, the previously induced current will exist for some time. Although exact values of the duration of these currents are not available, a specific observation may be of some interest.

On the morning of August 8, 1960, the wind velocity was about 0.5 m/sec from 220°. There was a current of 1 cm/sec at a depth of 20–30 cm and a current of 7.5 cm/sec at 2 m. A steady breeze of 3.5–4.0 m/sec from 290° came up quite suddenly. A series of drags was released immediately, and within 20 min the new wind stress began to dominate the currents at 20–30 cm. Release of 2-m drags showed a lapse time of 90 min until the new wind current became effective at this depth.

The horizontal temperature gradient in the water will produce a vertical variation in the pressure gradient. This in turn causes a vertical variation in the magnitude of the gradient current. During the period of current observations, temperature soundings were taken every two weeks. The horizontal temperature gradient in the upper water layers was less than 0.01°C/km in most cases. Analysis of these data shows that the relative

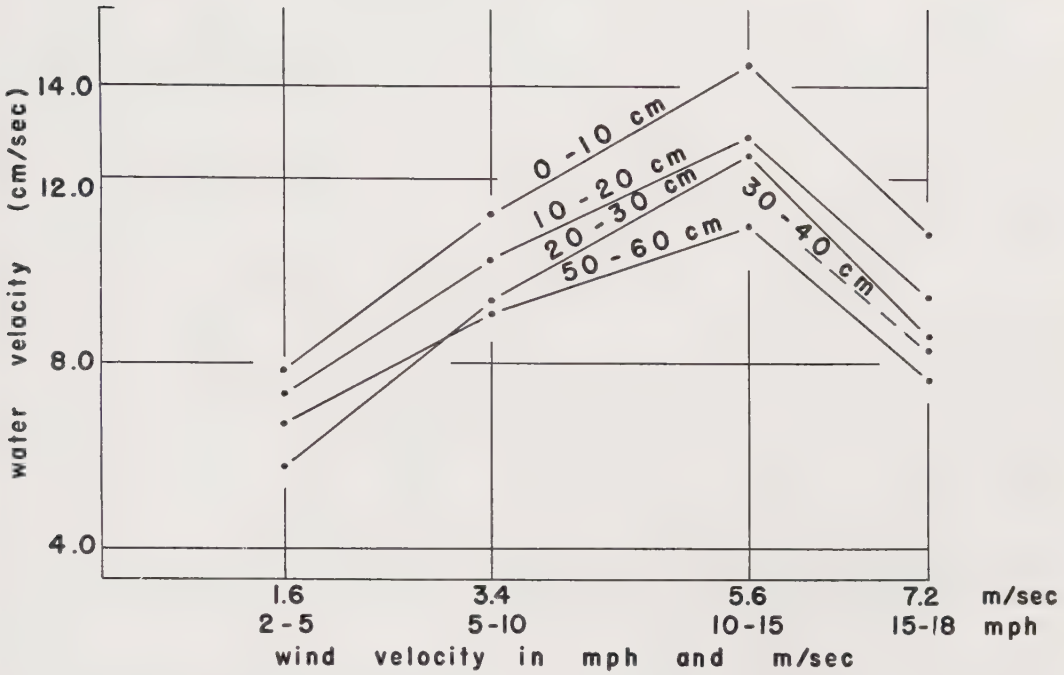

FIG. 2. The average water velocity at four levels as a function of wind velocity. The means were computed by averaging all water velocity observations within 5 mph wind velocity groups. Note the decrease of water velocity at all levels with higher wind speeds.

current variation within the layer studied did not exceed ±1 cm/sec.

Regression analysis applied to the wind velocity *vs.* water velocity scatter diagrams (Fig. 1) shows that below a certain wind speed, which we shall designate the *critical wind speed*, the lines of best fit for each water level intersect the water velocity axis at 4.9–5.8 cm/sec. The average value is 5.3 cm/sec. This implies that when the wind is calm, the average Lake Mendota current is 5.3 cm/sec in the upper 60 cm. When one considers all possible current producing factors, this figure appears to be reasonable. A more complete discussion of Figure 1 is given below.

4) Air and water temperatures were available for 55 of the 103 observations taken from 0–10 cm. Water temperatures higher than the temperature of the air will promote instability and convective activity. It was thought that this convection might affect the wind stress and thus show up as changes in the wind factor.

A χ^2 test of departure from the 0–10 cm regression line was made to see if there was a relationship between the departure and the temperature difference. The results were not significant even at the 50% level. Therefore, this variable was assumed to be of no importance in the analysis of the data.

Reasons for this result are not entirely clear, but a clue may be found in the work of Woodcock (1940). He found that for herring gulls to maintain continuous free-soaring patterns, it was necessary that

$$T_w - T_a \geqslant 2°\text{C}$$

where T_w is the water temperature and T_a is the air temperature. In only one case in 40 did flocks of gulls maintain soaring activity with a temperature difference of less than 2°C, and in this instance the value was only slightly less. Therefore, the 2°C spread may well be the critical temperature value for organized convective processes with wind speed below 7–8 m/sec.

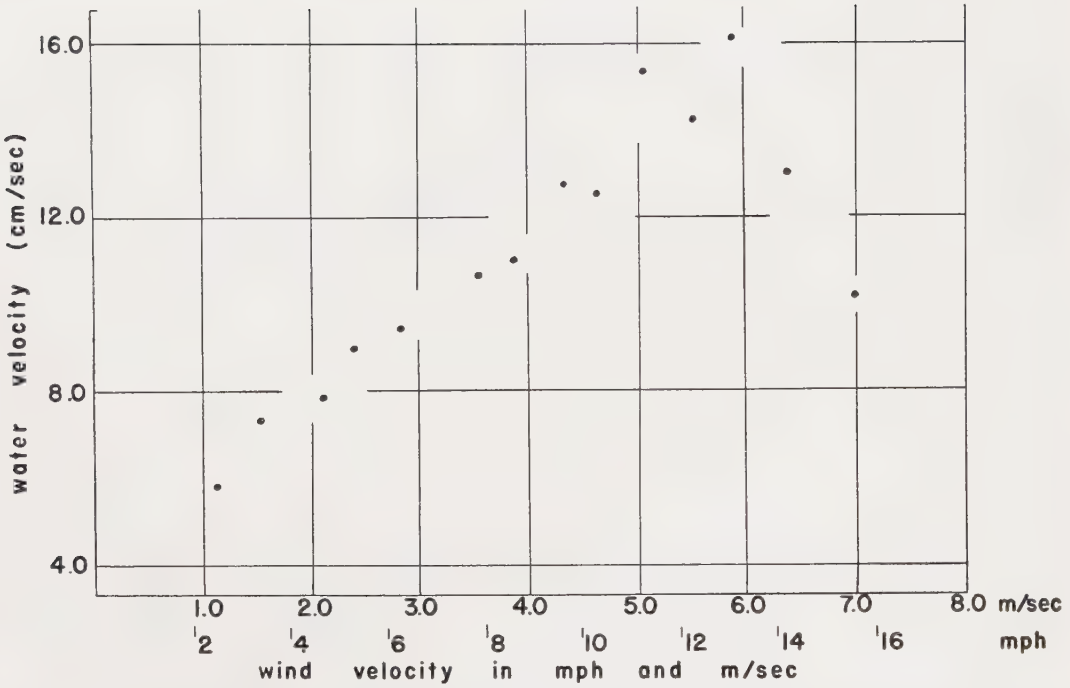

FIG. 3. A plot of overlapping median values of water velocity vs. velocity at the 0–10-cm depth. The moving medians were computed for 3-mph increments from 2 mph to 18 mph.

In the Lake Mendota studies, only 6 of the 55 cases of recorded temperatures showed

$$T_w - T_a \geqslant 2°\text{C}$$

and in only one case was

$$T_w - T_a > 3°\text{C}$$

Apparently the Mendota current observations were done under convectively inactive conditions. However, proof must await further empirical work on currents as a function of air-water temperature differences.

RESULTS OF LAKE MENDOTA OBSERVATIONS

The observations listed in Table 1 were taken at the stated water depths at wind velocities of 1–8 m/sec.

Figure 2 gives average water velocities at four depths as a function of wind velocity. The recorded wind velocity was measured in miles per hour. The means were computed by averaging all water velocity observations made with winds between 2–5 mph, 5–10 mph, 10–15 mph, and 15–18 mph. At a depth of 30–40 cm the only data available are at higher wind velocity, and the only mean entered is at wind velocities between 15–18 mph. Probably the most interesting feature of the diagram involves the decrease in current above the 12.5 mph (5.6 m/sec) mean wind speed.

Figures 3 and 4 give overlapping median values of the currents at 0–10-cm and 50–60-cm depths for various wind values. The moving medians were computed for 3-mph increments from 2 mph to 18 mph. Again it is quite evident that there is a change in the slope of the curve of water velocity vs. wind at 5–6 m/sec wind speed.

The diagrams of the mean wind *vs.* water

TABLE 1. *Number of observations taken at different water depths*

Depths (cm)	Number of cases
0–10	103
10–20	100
20–30	79
30–40	11
50–60	63

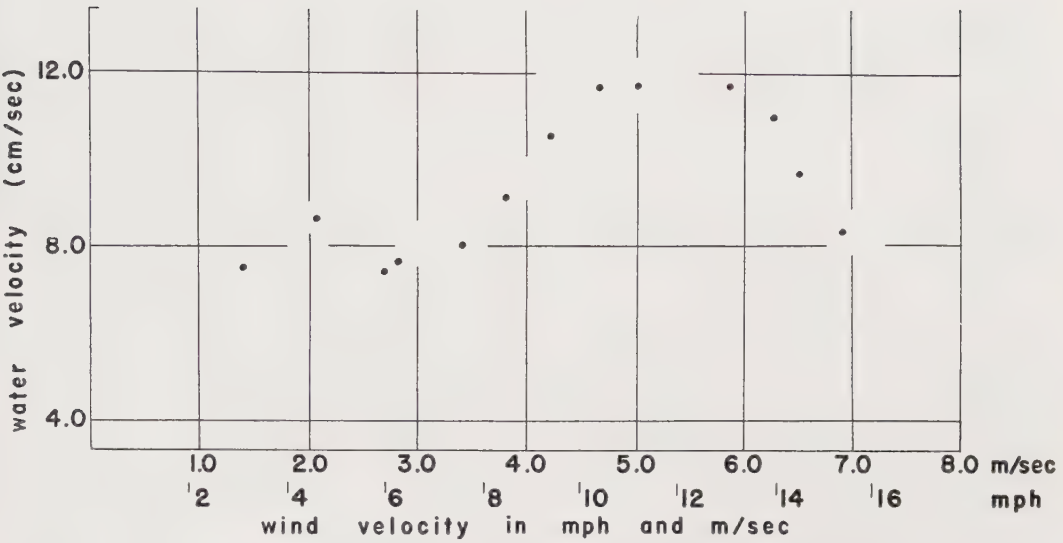

FIG. 4. Overlapping median values of water velocity vs. wind velocity at the 50–60-cm depth, obtained by the same method as in Figure 3. A decrease in water velocity is again evident above a wind speed of about 5–6 m/sec.

currents as well as the moving median plots show an increase in water velocity until a critical wind speed is reached. Above this wind speed the water velocity decreases. Therefore, regression lines were plotted for all water depths dividing the data into the wind speed ranges of 1–5.5 m/sec and 5.5–8.0 m/sec (Fig. 1). The regression lines were obtained by standard least square methods where:

$$V_w = a + b\,W$$

V_w is the water velocity, and W is the air velocity. (a) is the V_w axis intercept when W equals zero. (b) is the slope of the line. Below the critical wind speed (b) is the wind factor, if we define the wind factor to be the ratio of *wind-driven* current to wind speed, eliminating the current that would exist in the absence of wind, (a). Otherwise we must write

$$\frac{V_w}{W} = \frac{5.3}{W} + 0.013$$

as the average value of the wind factor for 0–60-cm water depth when the wind is below the critical speed. In this formula and those which follow V_w and W are in cm/sec, as in Table 2. Solution for (a), at winds below the critical wind speed, gives a value for the mean set or gradient current in cm/sec. The computed values of (a) and (b) for the individual levels using

$$V_w = a + b\,W$$

are given in Table 2.

In Figure 1 the 10–20-cm and 20–30-cm regression lines are reversed in position, above the critical wind speed, but the reversal is not significant. The (a) value is most likely either too low in the case of the 10–20-cm level, or too high for the 20–30-cm level. The over-all wind factor (b) for the

TABLE 2. *Values of the least square regression constants as a function of depth and wind speed range*

$V_w = a + b\,W$

where V_w = *water velocity in cm/sec and* W = *air velocity in cm/sec.*

Depth (cm)	Below critical wind speed		Above critical wind speed	
	a (cm/sec)	*b*[1]	*a* (cm/sec)	*b*
0–10	5.54	0.017	36.1	–0.037
10–20	5.57	0.013	35.7	–0.039
20–30	5.23	0.012	38.7	–0.043
50–60	4.87	0.012	40.5	–0.047

[1] This figure is the wind factor *if* only the directly wind-driven portion of the current is considered.

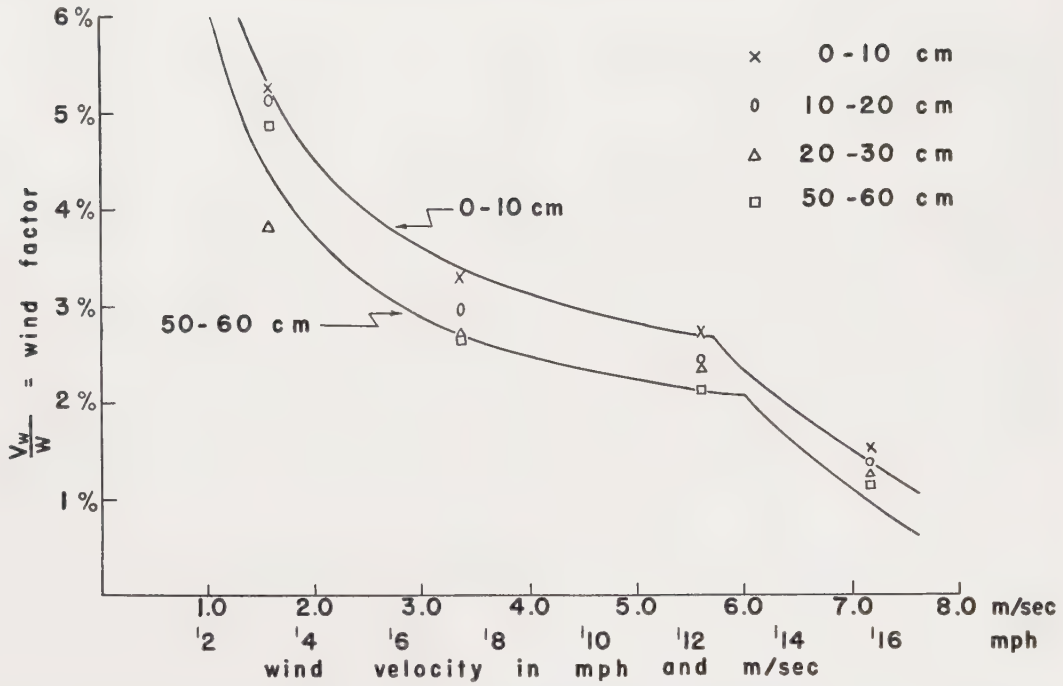

FIG. 5. Wind factor as a function of wind velocity. The curves are computed from the regression lines shown in Figure 1. The data points are values obtained by averaging all individually computed wind factor values within the wind ranges of 2–5, 5–10, 10–15, and 15–18 mph.

first 60 cm of water is 1.3% for the lower wind values. Above the critical wind speed the average wind factor takes the following form:

$$\frac{V_w}{W} = \frac{38.0 - 0.042\,W}{W} = \frac{38.0}{W} - 0.042$$

Of course, the water velocities cannot continue to decrease with increasing wind speed. Perhaps the wind factor at higher values follows a nonlinear instead of a linear pattern. Empirical confirmation will have to await more observations taken at higher winds.

BACKGROUND ON A CRITICAL WIND SPEED AS SHOWN BY ABRUPT CHANGES IN THE WIND FACTOR

Within the limits of the Kelvin-Helmholtz theory, a wind speed of 6–7 m/sec would equal the critical speed for transition from a hydrodynamically smooth to a hydrodynamically rough water surface.

Rossby (1936) also differentiated between two hydrodynamically distinct types of water surfaces. At low wind speeds he inferred that the water surface is a hydrodynamically smooth surface. At higher wind speeds it is hydrodynamically rough. He argued that with a rough surface the stress value would be about three times what it would be if the surface were smooth. The Rossby and Montgomery (1935) model implies a critical wind speed of 6–8 m/sec at indifferent stratification.

Proudman (1953), utilizing the work of W.

TABLE 3. *Critical wind speeds computed by regression analysis of wind speed vs. water speed. They are obtained by finding the intersection point of the two regression lines at each depth.*

Depth (cm)	Critical wind speed (m/sec)
0–10	5.7
10–20	5.7
20–30	6.1
50–60	5.9
Average	5.9

Thomson (1871), presents a mathematical treatment of the behavior of a surface of discontinuity of both density and current. Using specific values for contributing physical parameters, Proudman finds a minimum speed of instability (critical wind speed) of 6.5 m/sec.

Employing an empirical approach, Munk (1948) showed that in the upper water levels a critical wind speed does cause abrupt changes in physical processes. His paper includes the following findings:

1) The transition from a smooth sea to a sea covered by whitecaps appears at a wind speed of 5.5–7.9 m/sec, (Beaufort 4).
2) The resistance coefficient $\gamma^2 = \tau/(\rho' v^2)$ defined by Taylor (1916) undergoes a sharp change at a wind speed of about 7 m/sec. (Where τ = mechanical stress, v = wind speed at 15 m above the surface, ρ' = density of the air.)
3) According to Woodcock (1940) herring gull soaring patterns change at a wind speed of about 7 m/sec.
4) Sverdrup's (1946) graph of the evaporation coefficient vs. wind speed shows that at a speed of about 6 m/sec the evaporation coefficient changes abruptly from .08 to almost .15.

The Lake Mendota measurements show a decrease in current velocities at wind speeds above 5.7–6.1 m/sec. Langmuir (1937) also noted a decrease of water velocity with higher wind speeds, but offered no explanation for the phenomena. The critical wind speeds for given water depths are listed in Table 3. The averaged critical wind speed of 5.9 m/sec for current velocity change compares favorably with the values found using other types of physical processes.

CONCLUSION

At low wind speeds the average wind factor of 1.3% for the wind-driven currents in the upper 60 cm of water is somewhat less than the percentage given by most authors in the literature. However, previous investigators have rarely specified the depth at which their wind factor findings will apply nor have they eliminated currents other than those directly wind-driven. Also, other than a brief statement by Langmuir (1938) to the effect that he observed a decrease in currents at a higher wind speed, empirical investigations have not considered the possibilites of a critical wind speed with respect to water currents.

Regression analysis above the critical wind speed produces an average wind factor equation of:

$$\frac{V_w}{W} = \frac{38.0}{W} - 0.042$$

However, this assumes a linear relationship. Such a relationship cannot exist unless there is another point of discontinuity above wind speeds of 7.5 m/sec. This is unlikely, and, consequently, there is probably a nonlinear relationship between wind and water currents at higher wind values.

If the ratio of water velocity to wind velocity had been computed directly for each observation, the data points in Figure 5 would result after averaging over the given wind ranges. This figure presents the wind factor as usually defined as a function of wind velocity. The curves are computed from the regression lines shown in Figure 1. The data points are values obtained by averaging all individual wind factors within the wind ranges 2–5, 5–10, 10–15, and 15–18 mph.

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NOTES AND COMMENT

Effect of Hydrostatic Pressure Upon the Solubility of Gases[1]

Measurements of dissolved gases in natural settings are capable of yielding considerable information of geochemical interest, as has been pointed out, for example, by Richards (1957). The interpretation of such data often involves the use of the solubility of a particular gas under the particular local conditions of temperature, salinity, and pressure. It is important, therefore, that some apparent confusion surrounding the calculation of this quantity be clarified.

Solubility measurements of a gas are usually expressed in terms of an absorption coefficient, or a Henry's Law constant, relating the partial pressure of the gas above a solution to its concentration in the solution in the following manner:

$$P_i = k_i\,(P, T, S)\,[C_i] \qquad (1)$$

Here C_i is the concentration of the i species at some point in the solution, k_i the Henry's Law constant, and p_i the partial pressure of the i species above the solution. If Henry's Law is valid, k_i will be independent of p_i, but will in general be a function of the temperature, salinity, and of the total pressure. Laboratory measurements of this constant are made at some temperature and salinity, and at some "average" total pressure equal to the gaseous pressure upon the solution plus the "average" (but small) hydrostatic pressure of the experimental apparatus. Because of the great depths available in natural settings, the experimentally derived value for k_i may need to be considerably modified in applications to waters of scientific interest.

The dependence of a solubility constant upon total pressure is a second-order effect which may, however, be calculated in a straightforward manner (Guggenheim 1950). This calculation involves the partial molal volume of the gas in solution. These data are available for several gases (Kritchevsky and Iliinslaya 1945). A representative value is that of nitrogen, for which the partial molal volume at 25°C is 40 ml. From this we deduce that at a depth of one mile in pure water at 25°C, the Henry's Law constant for nitrogen is 1.28 of its value at the surface. In general, gas solubilities decrease somewhat at great depths, as may be seen from Table 1.

It has been implied occasionally (Ramsey 1960) that gas solubilities increase drastically with large hydrostatic pressure. Use is made of an equation due to Miyake (1951) which, in effect, considers the p_i of equation (1) to be the local pressure, as in a bubble constrained at some depth. The solubility calculated in this manner may thus be thought of as the critical concentration above which a bubble can, in principle, form. Although pertinent to the phenomenon of bubble formation, it is quite unrelated to the problem of solubility with respect to the surface. The confusion arises because the concept of solubility is meaningful only with respect to some specified gaseous state. This state is probably best taken to be an actual, existing gas, such as the atmosphere, rather than a hypothetical one, such as a potential bubble. The solubility of an atmospheric gas in an element of deep water, then, is not that calculated as in equilibrium with a bubble at that depth, but that concentration actually in equilibrium with the atmosphere. On the other hand, "critical concentration," or some equivalent, would then adequately describe Miyake's idea of the ability of a

Table 1. *Values of the inverse ratio of the Henry's Law constant in pure water of a gas at a given temperature and hydrostatic pressure, to the constant at the same temperature but at one atmosphere pressure*

Hydrostatic pressure (atmos.)	Nitrogen		Oxygen
	0°	25°	25°
100	.83	.85	.88
200	.69	.72	.77
300	.58	.61	.68
400	.48	.52	.60
500	.40	.44	.53

[1] This work was supported by the National Science Foundation under Grant NSF-G9437 to Amherst College. The author is grateful to Dr. Bruce B. Benson for several helpful discussions during the preparation of this manuscript.

dissolved gas to form bubbles at the particular local conditions.

Recent work in this laboratory has been concerned with the solution of atmospheric gases at the sea water-atmosphere interface. As the gas-laden water sinks from the surface, it will, if originally saturated, become supersaturated with respect to the surface, assuming constant temperature and salinity. The extent of this supersaturation is indicated by Table 1. Additional gases produced in photosynthetic regions or in anaeric waters (Richards and Benson) may be accommodated up to the limit given by Miyake's equation but will only add to the supersaturation. A vertical gradient in the chemical potential of each dissolved species will thus exist, and a small upward molecular diffusion of the excess gases should then occur.

The magnitude of such a diffusion current is expected to be small. It may well not be negligible, however, when the phenomenon of interest involves subtle differences in dissolved gas concentrations, as in anaeric regions, or a greatly expanded time scale, as in mass transport studies. The possible role of diffusion in such cases as a significant complicating process would seem to warrant, therefore, an investigation of the pertinent diffusion coefficients.

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A Plankton Sampler for Deep River Waters[1]

A vertical-closing modification of the Juday plankton trap (Fig. 1) has been constructed for taking plankton samples from the deeper waters of the Mississippi River. The inside dimensions of the box are 10 × 10 × 12 in., with a capacity of 20 L. The box is made of a strip of sheet brass 12 in. wide and 40 in. long. The sliding doors and fin are made of sheet brass. The doors are fitted with leather gaskets to make a tight fit when closed. Thick strips of plastic riveted to the edges of the door might have provided a better seal. The frame at each end is made of ⅝-in. right-angle extruded aluminum stock. All pieces are fastened together with brass bolts and nuts. Channeled aluminum runways for the sliding doors are bolted to the frame. The aluminum parts are made of stock available at many hardware stores.

The apparatus consists of a box (B) open at both ends, with a frame (FR) at each end to which is fastened channeled aluminum stock (CA) in which are fitted sliding doors. At the top of the frame on each end is a cabinet latch (CL) which engages the top edge of the door when it is drawn up. The apparatus is supported by cables (C) fastened to the upper corners of the box, and joined at the center to a ring (R) to which a suspended cable carrying a messenger (M) is attached. When the messenger is dropped, it strikes a pair of levers (L) which open the cabinet latches and release the doors. Lead weights (LW) force the doors to close. Heavier weights are needed in strong currents. With the apparatus in position with both doors open there is a considerable amount of drag. The large fin (F) serves to keep the box open to the current and a line attached to the front at the bottom of the box or at the top of the frame is needed to overcome the drag of the opened doors and keep the box vertical. A hole is cut in the bottom to which a brass

[1] Contribution No. 327 from the Department of Zoology, Oklahoma State University.

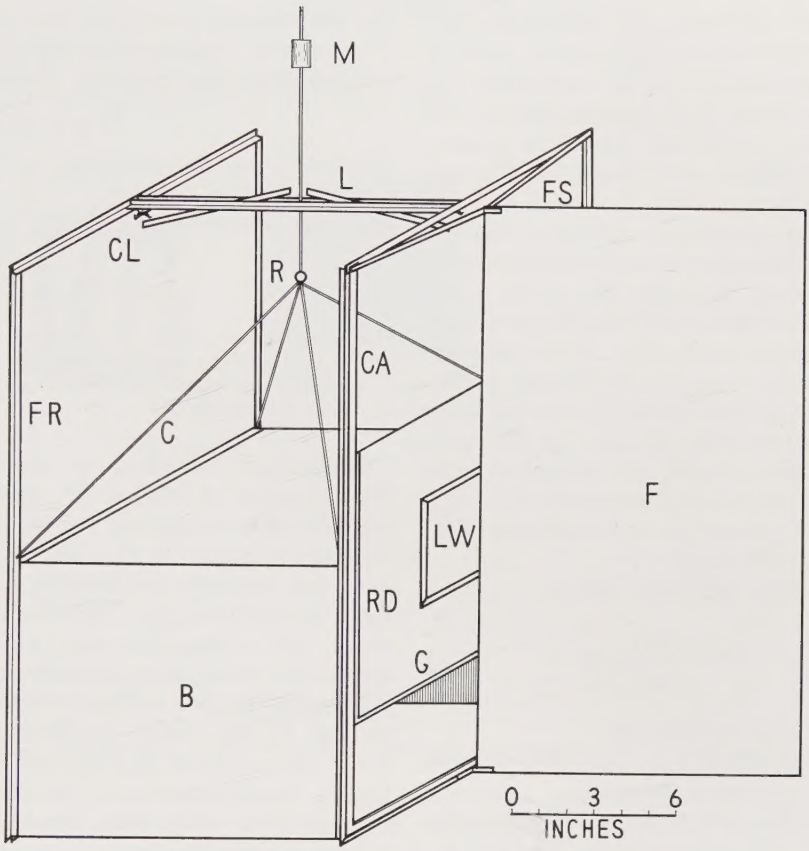

FIG. 1. Isometric drawing of 20-L plankton trap for subsurface sampling of river waters. B, box; C, supporting cable; CA, channeled piece to hold sliding door; CL, cabinet latch to hold sliding door open; F, stabilizing fin; FR, frame of ⅝-in. angle aluminum stock; FS, fin support; G, gasket on edge of sliding door; L, levers to actuate door catches; LW, lead weight on sliding door; M, sliding messenger; R, ring; RD, rear sliding door partly opened.

sleeve is soldered. The cup from a plankton net is attached to the sleeve. A large rubber stopper is placed in the hole until the sampler is drawn up out of the water. A cord passes from the stopper through a hole in the top of the box. By pulling the cord the rubber stopper can be dislodged and the water then passes out of the box through the plankton-net cup. A length of coiled spring can be fastened to the end of the cord to keep the rubber stopper pulled up out of the way while the box is being emptied.

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PHYTOPLANKTON COMMUNITIES, CO_2 AND O_2 CHANGES

In the paper on phytoplankton communities and associated CO_2 and O_2 changes by Jacob Verduin (1960), the author attempts the estimation of vertical eddy diffusivity from pH distribution data. These computations suffer from the omission of the very process that yielded the raw data, namely biological activity.

pH is a non-conservative variable whose value at any particular time and location is a function of biological activity (photosynthesis and respiration) and the physical

processes of advection and diffusion. If a horizontally homogeneous water mass is assumed, advection can be neglected. In the euphotic zone, both photosynthesis and diffusion are operating. However, photosynthesis decreases with depth, usually in a non-linear fashion, while in a mixed layer such as that described, diffusion may be expected to be approximately constant with depth. Photosynthesis for the entire water column can be estimated from the total shift of the pH curve with time. It would seem extremely risky, however, to estimate photosynthesis at a particular level in the presence of an unknown diffusion rate. At the same time, diffusion cannot be estimated from gradients alone when photosynthesis is also operating in part of the water column (presumably from 0 to 5 m).

The equation applicable here is

$$\frac{\delta s}{\delta t} = \frac{\delta}{\delta z}\left(\frac{A_z}{\rho} \cdot \frac{\delta s}{\delta z}\right) + P \qquad (1)$$

where $S = \mu$ moles CO_2/ml.

A_z = coefficient of eddy diffusivity in vertical direction

P = change in CO_2 concentration due to photosynthesis.

To compute A_z, P must be known for the levels involved and conversely to compute P at a particular level requires knowledge of A_z. Unfortunately, only data for daylight hours were given. Given the vertical distributions of pH at sundown and a few hours later, it would be possible to estimate A_z in the absence of P. Then, if wave and current conditions were not too different, the value of A_z obtained could be applied to the daylight data to estimate P at the various levels.

The assumption that any changes in pH at the 8-m level are due to diffusion is acceptable, but to use the vertical gradient between 3 and 5 m as that responsible for the diffusion across the 5-m plane cannot be accepted. Diffusion across a plane is due to the gradient across that plane, not above or below it. Actually, if the gradients across the plane, as given in Table 7 of Verduin's paper, are used, the computed values for eddy diffusion are not altered very much. However, the presence of two unknowns in equation (1) prevents evaluation of one without an independent determination of the other.

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Ragotzkie's criticism has some validity. My estimates of diffusivity contain several simplifying assumptions; the two mentioned by Ragotzkie are: 1) that the pH change at 8 m was entirely attributable to transport from the euphotic zone, thus both photosynthesis and respiration were neglected. It seems likely that photosynthesis at this depth was negligible, but respiration would cause a decline in pH, hence neglecting it would make our estimate of transport to the 8-m level a conservative one. We introduced a correction for respiration, based on nocturnal pH decline, into several sets of data. This complicated the equation considerably and did not change the observed diffusivity value importantly, so I omitted it from the example I published.

2) I assumed that the average gradient between 3–5 m was the "diffusion gradient" at the 5-m level. It is, of course, influenced by photosynthesis in such a way that the gradient will appear steeper than the true diffusion gradient, so this assumption also makes the estimate of diffusivity a conservative one. I believe our data have provided an estimate of vertical turbulence which is of the correct order of magnitude, but it probably errs on the conservative side. It is one of the highest values of average vertical turbulence published for any lake.

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